MAY 14 1918
UNIV. OF MICH. LIBRARY

PUBLISHED QUARTERLY AT 63.
OCTOBER, JANUARY, APRIL, JULY.

Entered at New York Post Office as Second Class Matter.

JOURNAL OF ANATOMY

(ORIGINALLY THE JOURNAL OF ANATOMY AND PHYSIOLOGY)

CONDUCTED, ON BEHALF OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND, BY

PROFESSOR THOMAS H. BRYCE, UNIVERSITY OF GLASGOW
PROFESSOR EDWARD FAWCETT, UNIVERSITY OF BRISTOL
PROFESSOR J. P. HILL, UNIVERSITY OF LONDON
PROFESSOR G. ELLIOT SMITH, UNIVERSITY OF MANCHESTER
PROFESSOR ARTHUR KEITH, ROYAL COLLEGE OF SURGEONS, LINCOLN'S-INN-FIELDS, LONDON, W.C.

(*All Communications relating to the Journal should be addressed to the* ACTING EDITOR, *Professor Keith.*)

VOL. LII.

PART II.

JANUARY 1918

LONDON: CHARLES GRIFFIN AND COMPANY, LIMITED, EXETER STREET, STRAND, W.C. 2 1918

Annual Subscription, 21s. post free.

BIOMETRIKA

A Journal for the Statistical Study of Biological Problems

Founded by W. F. R. WELDON, FRANCIS GALTON and KARL PEARSON. Edited by KARL PEARSON

Contents of Vol. XI, Part IV (May 1917)

I. W. R. Macdonell, Born October 16, 1852; Died May 15, 1916 (Notice with Portrait).

II. Further Supplementary Tables for Determining High Correlations from Tetrachoric Groupings. By Alice Lee, D.Sc.

III. On the Probable Error of Biserial η. By Karl Pearson, F.R.S. (With One Figure in the Text.)

IV. A Preliminary Report on some Breeding Experiments with Foxgloves. By Ernest Warren, D.Sc.

V. On the Distribution of the Correlation Coefficient in Small Samples. Appendix II to the Papers of "Student" and R. A. Fisher. A Co-operative Study by H. E. Soper, A. W. Young, B. M. Cave, A. Lee, and K. Pearson. (With Plates XXIV–XXVIII and Two Figures in the Text.)

Miscellanea:

(i) Tables for estimating the Probability that the Mean of a unique Sample of Observations lies between $-\infty$ and any given Distance of the Mean of the Population from which the Sample is drawn. By "Student."

(ii) On the Representation of Statistical Data. By L. Isserlis, D.Sc. (With Three Figures in the Text.)

(iii) Relation of the Mode, Median and Mean in Frequency Curves. By Arthur T. Doodson, M.Sc.

(iv) The Probable Error of a Mendelian Class Frequency. By Karl Pearson, F.R.S.

Biometrika appears about four times a year. A volume containing about 500 pages, with plates and tables, is issued annually.

The subscription price, payable in advance, is 30*s. net* per volume (post free); single numbers, 10*s. net*. Volumes I–XI (1902–17) complete, 30*s. net* per volume; bound in buckram, 37*s.* 6*d. net* per volume. Index to Volumes I to V, 2*s. net*. Subscriptions may be sent to C. F. CLAY, Cambridge University Press, Fetter Lane, London, E.C. 4, either direct or through any bookseller.

Till further notice, new subscribers to *Biometrika* may obtain Vols. I–XI together for £12 *net*.

ABDINE.
ABDINE.
ABDINE.

Meets a want keenly felt by medical gentlemen.
Is meant to take the place of the common effervescent powders, being more pleasant to taste, very mild laxative, and soothing to the stomach in cases of sickness. Contains no injurious drug.

Sold by most Chemists, in boxes containing 12 powders, price 1/6 per box.

AWARDED GOLD MEDAL, 1900.

DUNCAN M'GLASHAN, Chemist,
ABDINE WORKS, WESTFIELD ROAD, EDINBURGH.

JOURNAL OF ANATOMY

THE EARLIEST STAGES OF DEVELOPMENT OF THE BLOOD-VESSELS AND OF THE HEART IN FERRET EMBRYOS.

By CHUNG-CHING WANG, M.D., Ch.B. (Edin.), *Acting Lecturer and Demonstrator in Anatomy, University College, London; late Carnegie Research Fellow in Embryology, and Assistant in the Department of Anatomy, Edinburgh University.*

(*Continued from October Number.*)

STAGE IV.

This stage is represented by one embryo 2·5 mm. in length, the cranial extremity of which has been reconstructed in wax.

Description of the Plastic Reconstruction of the Heart and the Cranial Portion of a Ferret Embryo 2·5 mm. in Length with 12 Paired Somites. (F. Ap. 13/28/08.)

A plastic reconstruction of the cranial portion of this embryo has been made, which was exhibited, along with several other reconstructions of older specimens, before the Anatomical Section of the International Medical Congress at its meetings held in London in August 1913.

Technique.

The mother was killed with chloroform and the abdomen opened immediately. The whole uterus was removed and the embryo fixed *en bloc* with warm Zenker's fluid. It was afterwards washed in running water and transferred to industrial spirit coloured with iodine in the usual manner.

The embryo, with about half of the uterine wall attached to it, was stained in bulk with Meyer's acid hæmalum, and counterstained with eosine. After subsequent treatment in the usual way, the specimen was embedded in paraffin, trimmed and provided with guiding-lines. The embryo, which was exposed to view after the dorsal half of the uterine

wall was removed, was carefully measured before being fixed and stained, and was found to be 2·5 mm. in length, age being 14 days old approximately. It was then cut in serial sections with a thickness of 10 microns, and yielded 240 perfect sections, there being, therefore, a slight but uniform shrinkage of ·1 mm. The plane of section was almost directly transverse to the long axis of the embryo in caudo-cranial succession.

On microscopical examination the resulting sections are found to be in excellent quality, and present a perfect histological picture with frequent mitotic figures and a normal condition of the general contour of the epithelial linings of the various organs, vessels, and body spaces—all pointing to the specimen being normal.

Tracings of every section of the cranial end of the embryo were drawn with the aid of the projector apparatus at a magnification of 100 diameters, and these, in turn, were made into wax plates of 1 mm. in thickness. When the plates were cut out and methodically adjusted into position with careful manipulation of the guiding-lines, and in their numerical order, it was found that they superimposed one another most accurately, and that the structures faithfully took up their relative anatomical positions. After the model of the embryo had thus been built up, the original guiding-lines were dispensed with, but, to minimise any error that might arise in the subsequent division of the reconstruction into detachable blocks to expose to view the deeper organs, new guiding-lines were made on the surface of the reconstruction. The plates were then solidified and slightly smoothed, and the structures painted over with different colours to represent the various organs. The model is now to be seen at the Anatomical Department, Edinburgh University.

Such plastic reconstructions, generally known as Born's reconstruction, as has often been pointed out, are not to be considered as absolutely free from error even with the most accurate manipulation of the wax plates provided with the most reliable guiding-lines; for it has been noticed that the variations of temperature in the room at the time when the model is under the process of reconstruction, or even after the reconstruction is completed, materially alter, though in a small degree, the consistency of the wax employed, and therefore affect the model; but the results obtained with the Born's method are such as cannot be so conveniently produced by any other known method.

General Description.

It should be pointed out that the embryo under consideration came from the same uterus as the one of 13 somites described by Yeates ('15), to which references will be made hereafter.

The embryo is, in certain ways, similar to the human embryo described by Alexander Low ('08), which measures 2·6 mm. in length and exhibits 13–14 somites. Three visceral pouches can be distinguished, as in the case of Yeates' ('15) specimen, but there are only two external clefts in the specimen (figs. 21 and 25). In the latter respect the ferret embryo may be regarded as being in a somewhat younger stage of development than the human embryo described by Low, which shows three visceral clefts besides possessing an S-shaped heart tube. The brain flexure of the ferret embryo at this stage corresponds, in a measure, more to the ferret embryo of 13 somites described by Yeates and to the human embryo of 13 somites described by Ivan E. Wallin ('13) than to the one described by Low.

As in all of the embryos above quoted, but resembling more closely to the 4-mm. human embryo described by Bremer ('05–'06), the medullary tube opens to the exterior at its cranial and caudal extremities, the former (figs. 22, 25, and 27) with a slit-like but bent aperture over a distance of 28 sections, and the latter with an opening of equal length. This feature harmonises with the statement made in Keibel's *Normentafeln*, that in both the pig and the rabbit embryos the closure of the medullary tube is completed only after the formation of the head and neck bends. It may be mentioned here that the bucco-pharyngeal membrane is present (figs. 22 and 27), and that the rudiment of the nephric body is first seen opposite the 7th somite, and thereafter it is not separated from the paraxial and lateral mesoderm.

Somites.

Twelve pairs of well-formed somites are present. They were determined by careful counting under the microscope. The first formed somite is distinctly caudal to the otic plate by a distance of ·2 mm. As the ganglia are not yet well developed, it is futile to attempt, at this stage of development, to allot the different somites to their respective regions. Each somite has a uniform thick wall three or four cells in depth, enclosing a cavity (myocœl) which looks very distinct in the more caudal somites, but less so in those situated more cranially. Many of the nuclei, which lie near the cœlom of the somite, show definite signs of mitosis. The more cranially placed somites (fig. 23) are distinctly triangular in shape on cross section, with the apices pointing ventro-medially and the bases dorso-laterally, while the more caudal ones (fig. 24) are more or less quadrangular in outline.

Allantois.

The allantois may be described as having the appearance of a small diverticulum on the caudal end of the entodermal sac. Its caudal extremity

FIG. 21.—Dorsal view of plastic reconstruction of ferret embryo 2·5 mm. × 75.

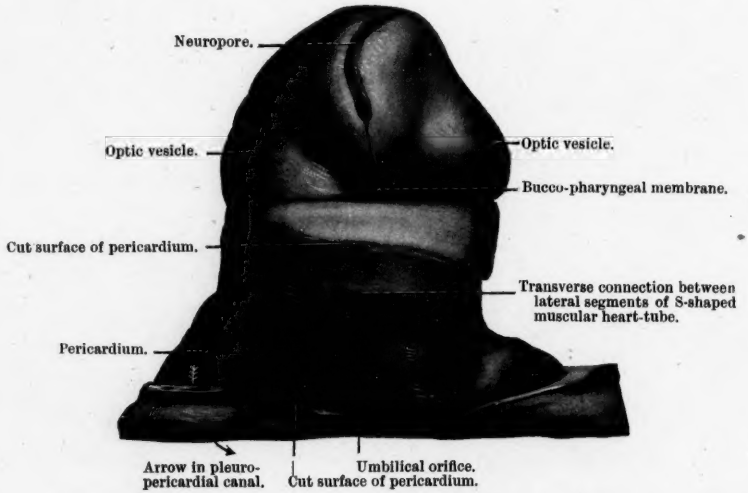


FIG. 22.—Ventral view of plastic reconstruction of ferret embryo 2·5 mm. × 75.

is, however, bifid, as noted by Yeates of London ('11); the bifidity includes both the entodermal and mesodermal components This mode of develop-

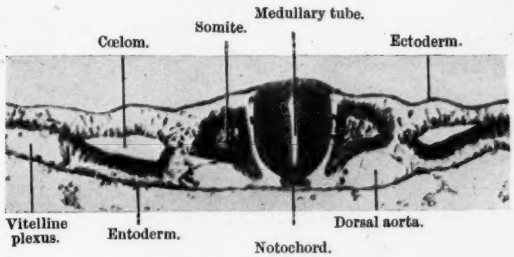


FIG. 23.—Transverse section through embryo. ×100.

ment of the allantoic cavity seems to occupy an intermediate position between that of the typical mammal and that of the lizard.

Nervous System.

The medullary tube, as already pointed out, is closed except at its cranial and caudal ends, where the cranial and caudal neuroporic apertures are present. The mesencephalon is flexed upon itself, in such a way as to bring the prosencephalon almost to a plane parallel with the long axis of

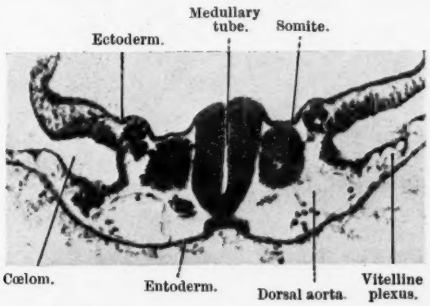


FIG. 24.—Transverse section through embryo. ×100.

the rhombencephalon, which merges, without any definite line of demarcation, into the spinal medullary tube (fig. 25). The pontine and cervical flexures are definitely absent in this specimen. The otic vesicle is represented only by a thickened plate of epithelium which shows no indication of invagination, and is situated ·2 mm. cranial to the first pair of somites

(*vide supra*). There is yet no lens thickening to be detected. The primary optic vesicle on each side is, however, well represented by a slight bulge of the lateral wall of the anterior portion of the prosencephalon of the corresponding side, much in the same way as in the specimen described by Yeates ('15).

When the whole series of the sections is examined under the high power of the microscope, the notochord is found to be free throughout its

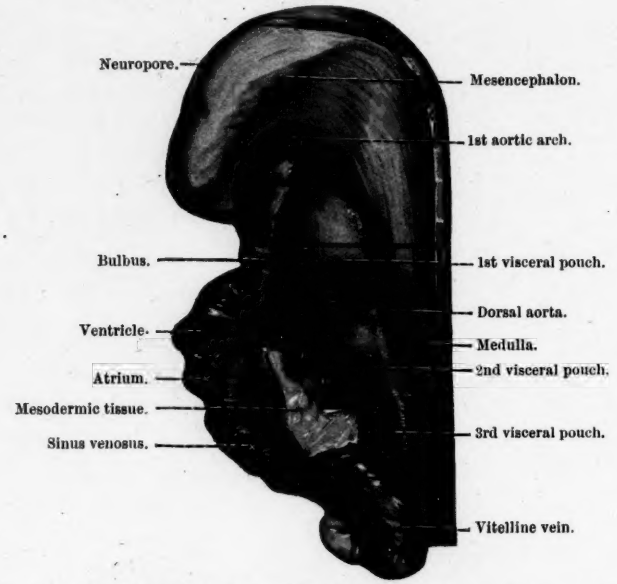


FIG. 25.—Lateral view of plastic reconstruction of ferret embryo 2·5 mm. × 100.

whole course, except at the cranial part, where it is still connected with the gut wall from a point opposite the first somite to the bucco-pharyngeal membrane, and at the caudal end, where it is connected with the entoderm from the level of the 7th somite to the end of the body of the embryo. The notochordal canal at this stage of development, as described by Mall ('12), Eternod ('95, '99), and Grosser ('13), is just discernible under the high power (fig. 26). In the ferret embryo of 13 somites, it is to be noted no lumen could be made out by Yeates ('15) in either the cranial or the caudal parts of the notochord. In places the cells of the notochord are arranged in two lateral masses which suggest the presence of bilateral symmetry (fig. 23). The cells of the chorda are comparatively large, oval, and clear.

Pericardium.

The reconstruction shows that at this stage of development the pericardial cavity is closed except at the dorsal part of its caudal extremity, where it communicates, on each side, with the pleuro-pericardial canals which are situated dorso-medial to the vitelline veins (figs. 22 and 30). The pericardium, measuring 875μ in width and 350μ in length, is reflected on to the two endothelial tubes on its dorsal aspect, forming the dorsal mesocardium, but ventrally there is not even the vestige of the ventral

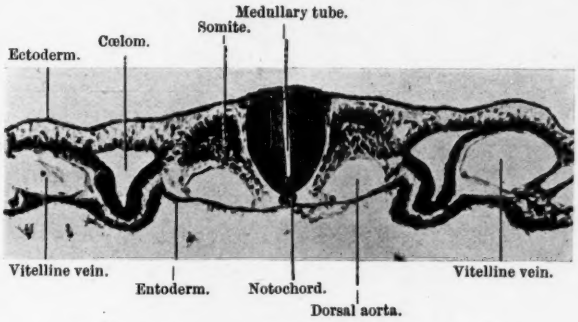


FIG. 26.—Transverse section through embryo. ×100.

mesocardium which, in birds and amphibians, is so conspicuously seen at this stage of development.

Heart.

With the ventral portion of the pericardium removed (fig. 22) it is obvious that the ventral aspect of the heart rudiment is separated in the caudal but larger portion of its extent into a right and left segment by a cranio-caudal sulcus. On each half there are also several transverse sulci, but the significance of these various sulci is rather obscure, as the segments marked out by them do not correspond, in any way, with the primary divisions of the heart tube, although at first sight it appears that the left segment is apparently atrial, and the right, ventricular. The fact that this appearance is deceptive becomes at once obvious when a portion of the muscular wall of the heart is removed (fig. 27); for it is then seen that within the lumen of the muscular tube, and separated from its wall by a more or less thick mass of loose mesodermic tissue, lie two endothelial tubes which are quite separate from one another in the whole of their extent (figs. 27 and 28*a*–*d*). Each endothelial tube can be followed caudally to the

septum transversum, where it is continuous with the corresponding vitelline vein immediately cranial to the umbilical orifice (figs. 27 and 28*a*), and cranially it is continuous with the first cephalo-aortic arch, which runs dorsally through the mandibular arch round the cranial border of the first visceral pouch (figs. 25, 27, and 29).

In the reconstruction (fig. 27) the muscular coat of the heart rudiment

FIG. 27.—Ventral view of ferret embryo 2·5 mm. with muscular wall of heart partially removed. ×100.

has been removed entirely on the left side but only partly on the right side. In this way the left endothelial tube is, therefore, fully exposed to view on its ventral and lateral aspects, and it exhibits clearly a very definite indication of separation into divisions which appear to indicate, in caudo-cranial succession, the positions of the sinus venosus, the sino-atrial canal, the atrium, the atrio-ventricular canal, the ventricle and the bulbus cordis (fig. 27).

The dilatation (figs. 25 and 27) which represents the sinus venosus

occupies the most caudal portion of the tube and is partly embedded in the substance of the septum transversum and partly projects into the

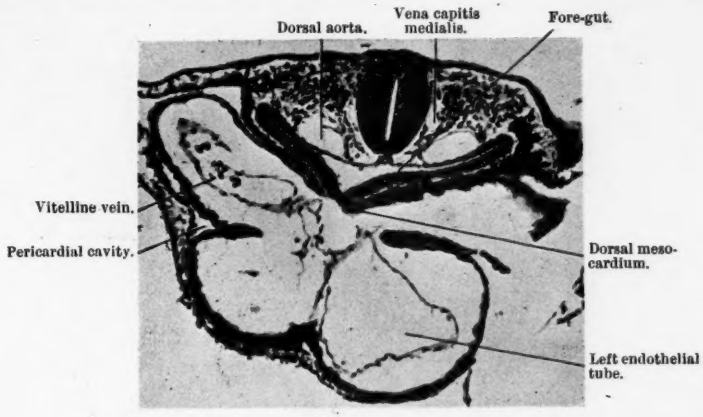


FIG. 28*a*.—Transverse section through heart region of 2·5 mm. ferret embryo. × 100.

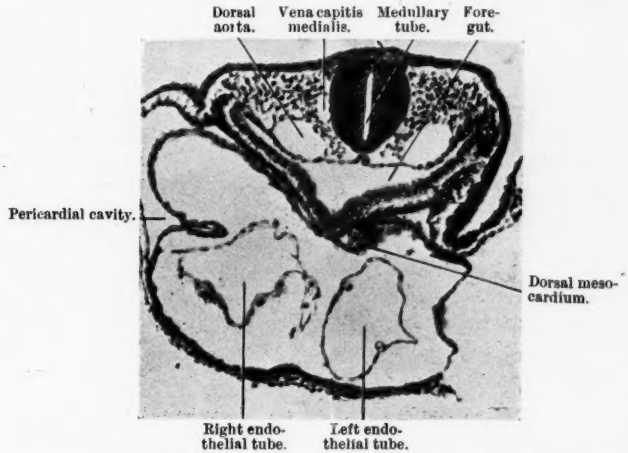


FIG. 28*b*.—Transverse section through heart region of 2·5-mm. ferret embryo. × 100.

pericardial cavity. At its caudal end near its dorsal aspect it receives the corresponding vitelline vein, which turns abruptly from the transverse to a caudo-cranial direction before it empties itself into the sinus venosus (fig. 27).

The constriction which indicates the position of the sino-atrial canal is distinctly marked laterally and dorsally (fig. 27). It is less conspicuous

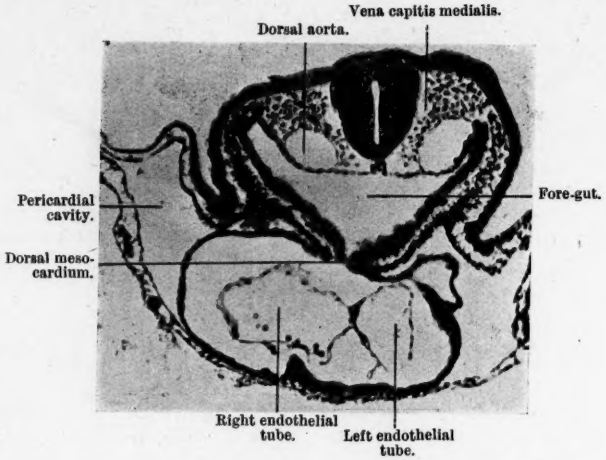


FIG. 28c.—Transverse section through heart region of 2·5-mm. ferret embryo. × 100.

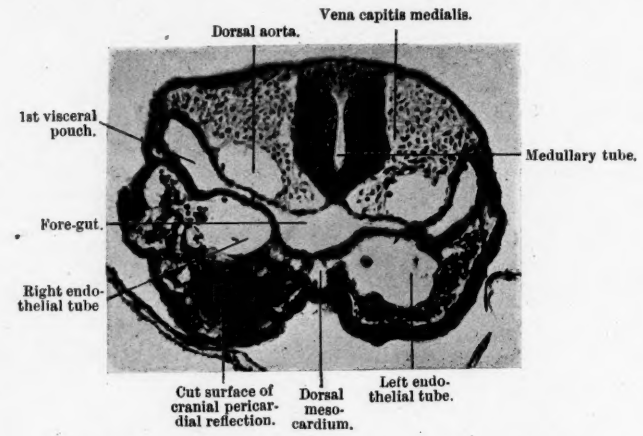


FIG. 28d.—Showing cranial pericardial reflection. × 100.

ventrally, and is altogether absent on the medial side of the tube. The dilatation (figs. 25 and 27) which takes the place of the atrium is comparatively small, and the constriction (fig. 27) which indicates the position

of the atrio-ventricular canal can easily be recognised on the medial and ventral aspects of the tube and slightly on the dorsal, but there is nothing to suggest a constriction on the lateral aspect in this situation (fig. 25).

The ventricle which is situated at the most cranial end of the endothelial tube is bent upon itself (fig. 27), and the most dependent point of the tube is the most ventral part of the ventricular portion (figs. 25 and 30). It is divided by a shallow depression, clearly recognisable on the lateral aspect (fig. 27), into a caudal and a cranial limb; the latter is separated by a somewhat oblique constriction from the bulbus cordis, which is bulged laterally and then turns cranially to be continuous with

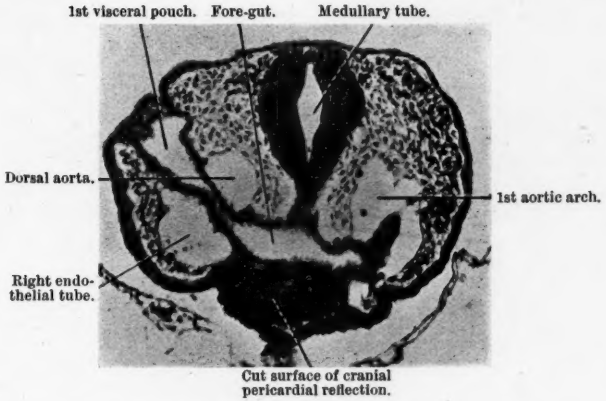


FIG. 29.—Showing first aortic arch. ×100.

the ventral aorta immediately below the caudal extremity of the ventral part of the first visceral pouch.

The right endothelial tube, which has not been fully exposed in the reconstruction, appears to present similar dilatations and constrictions, the outlines of which can be followed, to a certain extent, through the muscular covering, but, since in the model it is still covered in parts by muscular substance, the exact details cannot be worked out at present, and therefore no positive statement regarding it can be put forward. It is, however, more dorsally situated than the left tube (fig. 30); moreover, the whole heart is bent slightly towards the right side in the ventricular region (fig. 27).

The heart at this stage of development is attached to the dorsal wall of the pericardium (figs. 28*a-d*). There is positively no trace of a ventral mesocardium in the ferret embryo (a point already alluded to, but to be

fully discussed later), and the dorso-ventral length of the dorsal mesocardium is extremely short. The heart is applied closely to the ventral aspect of the pharynx in the region of the second visceral pouch.

In this communication it is not proposed to enter in detail into the development of the blood-vessels beyond the region of the heart, but, in passing, it is perhaps of interest to note that the ventral aorta communicates from the dorsal end of the bulbus cordis and runs cranially ventral to the first visceral pouch, then turns dorsally round the cranial border of the pharynx to form the first cephalo-aortic arch, and, finally,

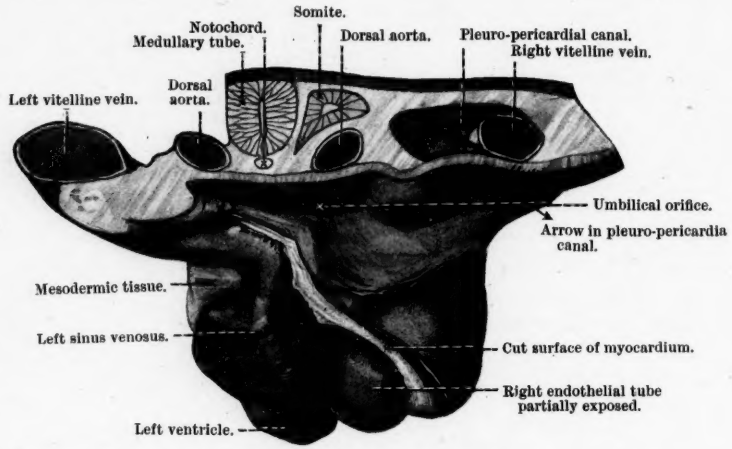


FIG. 30.—Caudal view of plastic reconstruction of ferret embryo 2·5 mm. × 100.

it pursues a course caudally along the dorsal wall of the fore-gut as the dorsal aorta (figs. 21 and 25). It is a relatively wide vessel, its calibre throughout being distinctly greater than that of the bulbus cordis.

Immediately dorsal to the dorsal aorta there is situated on each side of the embryo a series of apparently isolated sections of a minute blood-vessel (figs. 28*a-d*). These capillaries lie close against the medullary tube. This vessel appears to be the vena capitis medialis of Grosser ('95), which Miss Parker ('15) also has found to be present in her Stage III. *Perameles nasuta* 7·5 mm.

Intersegmental offshoots from the dorsal aortæ in the region of the caudal somites are described by Miss Parker in *Perameles nasuta*, but no such offshoots from the dorsal aortæ were present in the ferret specimen under consideration. In the caudal region of the embryo, the

two dorsal aortæ become continuous with the vitelline arteries, which spread themselves out in a plexiform manner on the wall of the yolk-sac (fig. 24). This stage of development of the dorsal aorta in the ferret agrees, in some ways, with the 1·3-mm. human embryo described by Eternod ('95, '99).

The vitelline vein (fig. 27), which opens into the caudal end of the sinus venosus, so far as it lies on the embryonic region, runs at first transversely towards the median plane in the substance of the septum transversum immediately cranial to the umbilical orifice. As it approaches the median plane it changes its course suddenly, making a sharp bend upon itself cranially, and terminates, as has already been indicated, in the dorsal extremity of the caudal part of the corresponding sinus venosus. It is applied so closely to the margin of the umbilical orifice that its caudal border causes a distinct bulging of the boundary of the orifice (fig. 27).

For the sake of comparison, and for the purpose of bringing out the chief differences, as far as the development of the heart is concerned, between this specimen and that of Yeates ('15), the description of the endothelial tubes of the latter given by Yeates might be quoted: "As the endothelial tubes course through the primitive cavity of the heart (the primitive cavity of the heart means the muscular tube—the myoepicardium) they are separated by a variable but distinct interval from the myoepicardium The myoepicardial tube has previously been stated to present constrictions at each extremity, at the sinuatrial junction and at the atrio-ventricular canal. The endothelial tubes present corresponding constrictions. In the region of these constrictions the endothelial tubes are relatively close to the primitive myoepicardium, whilst they gradually recede from the heart wall as the middle of each of the three primitive cavities of the muscular heart is approached. In other words, the muscular cavity is more expanded, and the endothelial is more tubular between the constrictions. The endothelial tubes are in contact medianly in the cranial two-thirds of the atrium, in the ventricle and in the region of the bulbus. In the atrio-ventricular canal they are not only in contact but have fused and are partially absorbed, so that their cavities communicate across the median plane. On the other hand, in the region of the sinus venosus and of the truncus, the tubes are free and separate from each other. The portions of the tubes which are in contact within the atrium are connected by delicate endothelial strands with the inner aspect of the ventral wall of the atrium along the crest of the irregular ridge, which has been spoken of as the remains of the primitive cardiac septum. The ventricular limbs of the endothelial tubes are subdivided into ventricle, bulbus

cordis, and truncus arteriosus by two faintly marked constrictions. The endothelial heart, therefore, consists of not only sinus venosus, atrium, and ventricle, as in the muscular heart, but also of bulbus cordis and truncus arteriosus."

It will be noticed, then, that Yeates' specimen is decidedly in a more advanced stage of development, since the two endothelial tubes have partially fused in the region of the atrio-ventricular canal, much in the same way as the Stage V. specimen, to be immediately described.

Subdivisions of both of the endothelial tubes into sinus venosus, atrium, ventricle, bulbus cordis, and truncus arteriosus have been observed also by Yeates in his specimen; but, unlike those of the Stage IV. 2·5-mm. ferret embryo, these subdivisions correspond in the main in positions to those exhibited in the muscular (myoepicardial) wall of the heart tube. One point which is clear is that the endothelial tubes differentiate into their various subdivisions more completely than the muscular tube.

It should be pointed out that the second aortic arch in Yeates' specimen has already made its appearance.

It is to be noted that, as far as the external appearance of the heart is concerned, the ferret embryo at this stage of development shows certain prominent features which are in many respects identical with those of the dog of a similar stage of development, and which have been investigated by Bonnet ('01). In his paper it has not been possible to find a comprehensive description of the development of the heart of the dog. In fig. vi. (*Anat. Hefte*, 1901, Bd. xvi.) Bonnet depicted a dog embryo 5·7 mm. long with 10 somites. There the heart is represented by two endothelial tubes which are distinctly separated from one another and are both bent towards the right side in the ventricular region; each endothelial tube has, for its caudal continuity, the corresponding vitelline vein, which runs latero-medially and at the same time cranially towards the sinus venosus. There seems to be no distinctive demarcation between the sinus venosus and the atrium, but between the atrium and the ventricle there is a constriction both on the lateral side and the medial side. The ventricle looks very much dilated in the figure, so much so that, when viewed from its ventral aspect, the whole heart appears to be formed by the distended ventricle, with the bulbus cordis and atrium attached to it cranially and caudally respectively as mere appendages. The bulbus cordis is clearly constricted off from the ventricle, and its calibre is barely one-third of that of the ventricle.

Stage V.

The material for this stage consists of one embryo which measures 3·14 mm. in length.

Description of the Graphic Reconstruction of the Heart of a Ferret Embryo 3·14 mm. in Length with 13-14 Somites. (F. 15d. (e).)

The general development of this embryo is so similar to that of the Stage IV. specimen as to merit no separate description.

The specimen is slightly older than the Stage IV. ferret embryo. As in the case of the other embryos described, the state of preservation of this embryo is perfect. In length it undoubtedly exceeds the Stage IV. specimen, but when other measurements are taken, the fact is revealed that the embryo in question is relatively a small one. The pericardial cavity measures 400μ in its cranio-caudal diameter and 840μ from side to side.

No plastic reconstruction of this embryo has been made. The graphic reconstruction of the heart, however, shows that the two endothelial tubes have united in part of their extent (figs. 31 and 32). The fused portion, extending through some sixteen sections of 10μ each, appears to be the ventricular part and lies more to the right side (figs. 31 and 32). Cranially the fused ventricle divides into two vessels, each of which represents the bulbus cordis (figs. 31 and 32) and becomes continuous with its corresponding dorsal aorta by looping round the cranial end of the pharynx, thus constituting the first cephalo-aortic arch (fig. 31). The paired atria run into the fused ventricle cranially, and each receives its sinus venosus caudally (fig. 34).

The vitelline veins are very much in the same stage of development as those observed in Stage IV. (compare figs. 27 and 31). The right vein pursues a more transverse course latero-medially, and terminates at its corresponding sinus venosus. In this, as in the preceding specimens, there is no trace of a ventral mesocardium. The dorsal mesocardium is, however, present in this specimen (figs. 32, 33, and 34).

It may be observed that at this stage of development the ferret heart, though resembling very closely the heart of the Stage V. *Perameles obesula* (19, viii., '03) described by Miss Parker, yet differs from it in many respects. In both cases the two endothelial tubes have partly fused. In the ferret the fusion occurs in the ventricular region (fig. 31). In the *Perameles obesula*, according to Miss Parker, the bulbus is the only portion of the heart in which the endothelial tubes have actually fused at this stage.

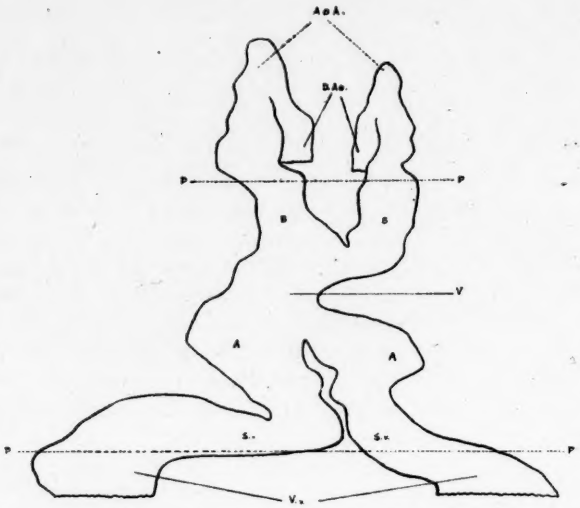


FIG. 31.—Graphic reconstruction of the heart of ferret embryo 3·14 mm., ventral view. ×100

Ao.A., aortic arch; D.Ao., dorsal aorta; B., bulbus cordis; A., atrium; S.v., sinus venosus; P., pericardial reflection; V.v., vitelline vein; V., ventricles (fused).

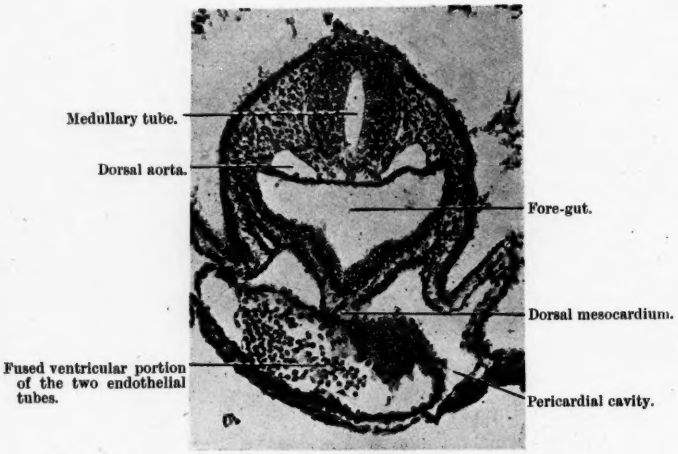


FIG. 32.—Transverse section through fused ventricular region of 3·14-mm. ferret embryo. ×100.

Asymmetry of the two endothelial tubes has also been noted in Parameles embryos. Miss Parker observes that whilst the left heart tube

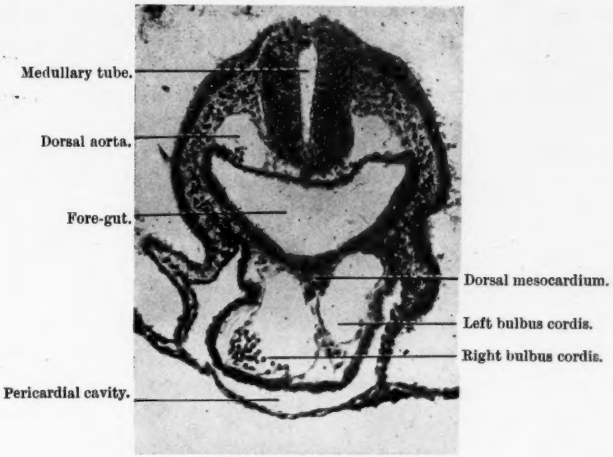


FIG. 33.—Transverse section through bulbus cordis. × 100.

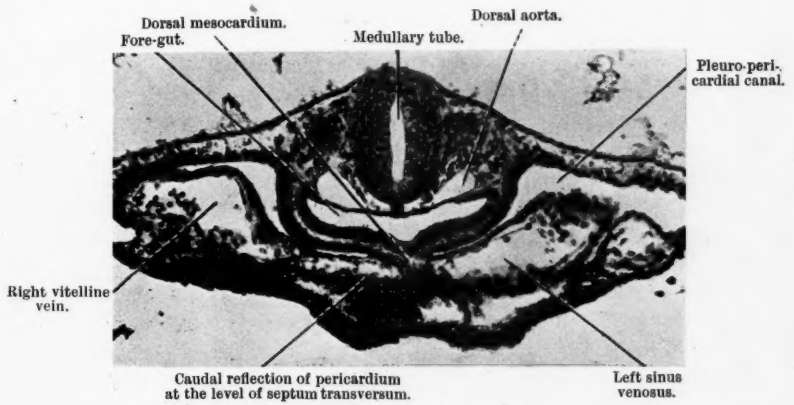


FIG. 34.—Transverse section through sinus venosus. × 100.

is practically straight, the right tube shows well-marked curvatures. In the ferret it has been found that the two tubes, prior to fusion, appear to have been shifted as a whole towards the right side (fig. 27), and that they remain in this position even after partial fusion has taken place (fig. 31).

Two pairs of aortic arches are found arising from the fused bulbus in the Perameles embryo, but only one pair of vessels can be recognised in the ferret embryo at this stage, and these come from the yet unfused bulbus (fig. 31). In both instances the ventricular portion is the most dependent part of the endothelial tubes.

Stage VI. *Macropus ruficollis* 5·2 mm. of Miss Parker is distinctly older and is in a more advanced stage of development than the Stage V. ferret embryo, but it is interesting to note that in Macropus the right and left heart tubes are fused *except in the region of the sinus venosus*, where they remain separate. Three pairs of aortic arches are described. The fused heart has already begun to acquire the S-shaped curvature, so that the bulbus arteriosus lies dorsal to the cephalic extremity of the ventricle. The bulbus arteriosus is continued into a short median ventral aorta which bifurcates to form the first pair of aortic arches. The second and third pairs of aortic arches arise from the median ventral aorta immediately caudal to its bifurcation. The atrial limb of the S is carried into position dorsal to the ventricle. On the other hand, in the ferret of 3·14 mm. the two heart tubes are only fused in the middle parts of their extents.

Discussion.

Origin of Blood Cells and Vessels.

The transformation of the blood-cells into red and white corpuscles lies outside the scope of the present communication, in which the developmental relationships which the blood-cells have in common with the vascular endothelium will alone be considered.

In the paragraph dealing with the development of the extra-embryonic vascular rudiments in mammals, it has been pointed out that in embryos of the higher vertebrates the earliest vascular rudiments have invariably been described by most authors as appearing, at first, in the form of localised cell cords ("angioblast" of His). Thus far all observations on this point incline to support the work of His ('00).

Further, in the literature of the past twenty-five years there are numerous descriptions and illustrations of the origin of blood-cells from the vascular linings. In 1892 Schmidt described the transformation of individual endothelial cells into white and red blood corpuscles. In support of Schmidt's view, Maximow ('09) states that the endothelial cells and blood-cells are closely related and arise from a common stem-cell in the blood islands, and may continue to do so from such a cell during later development.

The most damaging evidence against Maximow's view is to be found

in the recent work of Stockard ('15), who, after having conducted a series of experiments on Fundulus, comes to the conclusion that endothelial lining of vessels is utterly incapable of giving rise to any form of blood-cells, and that vascular endothelium arises *in loco* in many parts of the embryonic body in which blood-cell rudiments are not present.

If Stockard's view is correct, it necessarily follows that, even if the two groups of cells have a common origin, they are not interchangeable nor can one replace the other: nevertheless it is the common opinion, based upon the results of many investigators, that the angioblast cells produce both blood-cells and endothelium, but there is no agreement as to whether the angioblast cells are derived from mesoderm or from entoderm. Nearly all investigators in this field of work have assumed that blood cells and vessels have a common origin which some attribute to the mesoderm and others to the entoderm.

The facts now to be recorded do not support the view of a common angioblastic origin of both endothelium and blood-cells, and in this communication the term angioblast will be restricted to the progenitors of the blood-cells.

It has been pointed out that in the ferret embryos, Stage I. (*a*) and Stage II. (*b*) (figs. 1, 15*b*, 17*a* and *b*) it is possible to identify mitotic division in the entodermal cells in the neighbourhood of angioblastic clusters, and there is no evidence to show that, in the ferret, endothelial cells are capable of giving rise to blood-cells. In figs. 2*a*, *b*, 3, 4, 5, and 15*a* it is to be observed that angioblast cells are in abundance on the yolk-sac. These are frequently adherent to the entodermal cells, which, if not in direct protoplasmic continuity with the blood-cells, are, in many cases, in close contact with them. It is to be further noted that where the apposition of these cells is intimate, it is impossible to distinguish the angioblast cells from many of the entodermal cells, the nuclei, size, and shape of the two kinds of cells having a close resemblance. On the other hand, a great dissimilarity exists between the blood-cells and the neighbouring mesodermal cells, for in the former the cells are, without exception, spheroidal in shape, their nuclei are large, staining more deeply, and the protoplasm is comparatively small in amount; whilst in the latter, the cells are usually spindle-shaped, their nuclei have mostly differentiated and taken on a lighter stain (figs. 3, 4, 5, and 15*a*). Furthermore, in the ferret embryos angioblast cells have been demonstrated in regions of the yolk-sac where invasion of the mesoderm has not yet taken place. The above facts appear to indicate that, in the ferret at least, if not in all the other mammals, the origin of angioblast cells from the entoderm is highly probable.

With regard to the genetic origin of the vascular endothelium, numerous investigators have recorded wandering mesenchymal cells upon the yolk-sac. Stockard ('15) claims that in Fundulus these wandering mesenchymal cells ultimately give rise to four different kinds of cells—the endothelial cells, the black chromatophores, the brown chromatophores, and the blood-cells.

Another current view is that after the so-called "angioblast" has made its appearance, the vascular endothelium arises from the cells of the blood islands by a rearrangement of the peripheral cells of the blood islands to form lining endothelium and the central ones to remain as blood-cells, and that further extension of the endothelium is brought about by buddings of the endothelium which appear, at first, as solid cords but later become hollow. There is so far no evidence to show that the peripheral cells of the angioblast group in the ferret are capable of being transformed into endothelial cells. It is to be noted that in the ferret, endothelial cells, whether in the form of solid cords or grouped together with a lumen, are invariably spindle-shaped from the very beginning.

Ziegler ('87), as will be remembered, maintains that the system of blood-vessels and that of the lymphatic vessels are produced from the remnants of the blastocœl which remain behind as vessels, lacunæ, or interstices. Felix ('97), however, inclines to the belief that the circulatory system is, from a developmental point of view, closely related with the cœlom.

In connection with this question Stockard ('15) states: "The vessels arising from independent mesenchymal cells in the space of the blastocœl in the teleost yolk-sac entirely overthrow any notion that vessels arise ontogenetically as portions of the cœlomic epithelium. The vascular lumen is originally continuous with the primary body cavity, the segmentation cavity, and never with the secondary body cavity or cœlomic cavity."

It is clear that these authors agree, at least, that the origin of the endothelium is from the mesoderm. In the ferret it is possible to demonstrate that endothelial cells take their origin from the splanchnic layer of the mesoderm. In some of the sections of the ferret embryo of Stage II. (*a*) (figs. 10*a–d*) there are indications to support the view of Felix ('97) that portions of the cœlomic space surrounded by mesoderm may be cut off to form vascular endothelium and to lie between the mesoderm and entoderm.

The opinion that endothelium develops independently of blood-cells is furthered strengthened by the observations of Stockard ('15), who finds that vascular endothelium arises *in loco* in many parts of the embryonic body of the Fundulus, in which blood-cell rudiments are not present, and that independent blood islands, having no connection with the intermediate

cell-mass, are found on the yolk-sac, and even in extremely young embryos blood islands may appear on the ventral yolk surface at a great distance away from the intermediate cell-mass. He maintains, also, that early blood islands are invariably destitute of endothelial walls. Though favouring the view that vascular endothelium and blood-cells are independent of each other in their mode of development, Stockard firmly believes that both types of cells are derived from wandering mesenchymal cells. This author summarises his statement by saying: "The differences among the four types (endothelial cells, black chromatophores, brown chromatophores, and blood-cells) produced are from the standpoint of our present knowledge in all probability due to the potential differences among the apparently similar mesenchymal cells from which they arose. The four types including endothelial cells and erythrocytes we must consider from an embryological standpoint as arising from different mesenchymal anlagen."

It will be observed then that Stockard, whilst admitting, on the one hand, (*a*) that endothelial cells are quite different from blood-cells in shape, in position, and in the period of migration; (*b*) that the former develop independently of the latter; and (*c*) that blood-cells when first formed are devoid of endothelial surroundings, claims, on the other hand, that both types of cells have a common parent trunk—the wandering mesenchymal cells. In the Fundulus this is perhaps true, but the evidence produced by the ferret shows the conditions are not the same.

In the ferret there are indications to show that vascular endothelium is mesodermic in origin and that blood-cells are, at all events in the first instance, derived solely, by proliferation, from entodermal cells. Such being the case, it is obvious that the sources of origin of the blood-cells and vascular endothelium are distinct, and that these two different vascular rudiments cannot be considered to have a common origin.

If the biphyletic origin of blood-cells and vascular endothelium is to be accepted, two more points still remain to be solved, namely, how, when, and where the first blood-cells enter the circulation. This has been variously described not only in embryos of different species but probably even among embryos of the same species. Ziegler thinks, however, that just beyond the lateral plates in the plasma-filled spaces of the yolk-sac which lie between the periblast and ectoderm, the first blood-cells project into the circulation. Stockard describes that in Fundulus embryos the earliest blood-cell formation occurs in the yolk-sac blood islands. The cells in these islands continue to divide until they become surrounded by endothelium. As to how these blood-cells are provided with endothelial covering, Stockard makes the following statement: "A growing vascular tip may be observed at certain stages to come in contact with a group of

erythroblasts, or actually a blood island unsurrounded by vascular endothelium. The tip of the vessel seems to disorganise to some extent, and its cellular elements slowly surround the group of corpuscles which are later taken into the circulation as the current becomes established in the including vessel."

Unfortunately the ferret embryos, at present worked upon, provide no definite evidence on this point, but it is quite clear that angioblast cells are formed outside the embryonic area, and that blood-vessels are formed inside the embryonic area, and are at first devoid of blood corpuscles. Moreover, it has been pointed out that there is no evidence in the very young embryos dealt with that any blood corpuscles are formed by division of or budding from the endothelial walls of the independently formed blood-vessels. It would appear therefore that the earliest blood-cells probably enter the embryo from the periphery.

Intra-Embryonic Blood-Vessels.

In the review of the literature on the subject of the origin of the intra-embryonic blood-vessels, it has already been indicated that the problem has proved to be one of the most difficult in the development of the vertebrate animals. Numerous conflicting views have been advanced regarding the precise mode of the origin of the intra-embryonic blood-vessels. Thus His ('00) and Hertwig ('92) have associated themselves with the theory that the early blood-vessels in the body of the embryo are formed by a budding or ingrowth of the endothelial lining of the vessels from the extra-embryonic vascular area, and Sobotta ('02) supports the belief that vessels in the embryo develop *in situ*, and those on the wall of the yolk-sac are secondary as a result of an outgrowth from the intra-embryonic blood-vessels. Rabl ('86), on the other hand, pointed out the possibility of the vessels of, at least, the cranial region, if not the whole vascular system of the embryo, having been formed by the extension of the paired heart rudiments when these are developed. Recently Rückert and Mollier ('06) maintain that the embryonic vascular system, or at least a part of it, arises *in situ* from the mesoderm of the embryo. Felix ('97) states that in birds, the aorta and certain veniplexuses all arise *in loco*.

The question is therefore still open, and each view invites further criticisms or support. In birds the caudal portion of the dorsal aorta is, according to Vialleton ('92), His ('00), and Evans ('09), formed from the medial margin of the vitelline plexus which has grown into the embryo in the manner already indicated in the beginning of this communication. In the ferret, Stage II. (*a*), 1·97 mm., it has been found that the caudal portion of the dorsal aorta has established its communication with the

vitelline plexus. Precisely how the caudal end of the dorsal aorta in the ferret is developed, no definite statement can be made, but as far as evidence goes, it is probable that this part of the dorsal aorta arises much in the same way as described by Vialleton ('92) and His ('00).

For the development of the cranial portion of the dorsal aorta, on the other hand, various opposite views are held. His ('00) attributes it to the result of a further growth of the same extra-embryonic vitelline plexus which forms the caudal part of the aorta, but which is reduced to a capillary chain growing cranially, eventually turning ventrally over the blind end of the fore-gut and fusing with the cranial portion of the heart tubes. In support of this theory Lewis ('04) affirms that all intra-embryonic blood-vessels of rabbits are apparently derived as offshoots from the extra-embryonic network of vessels in the splanchnopleure of the yolk-sac, the vitelline plexus ending medially in the embryo in the form of two vessels —the dorsal aortæ. Quite recently Bremer ('12) states that in the rabbit embryo of 5 somites, the dorsal aorta, the first aortic arch, the conus arteriosus, and the lateral heart are all parts of an original network of angioblastic cords derived from the extra-embryonic plexus of blood-vessels.

Rückert and Mollier ('06) maintain that the cranial portion of the aorta is developed *in situ* from the mesodermic cells of the lateral plate of the mesoderm of the cranial region of the embryo. In support of the autochthyonic origin of the cranial portion of the dorsal aorta, the work of Huntington ('10, '14) and M'Clure ('10, '12) may be cited. Recently this view is further strengthened by the results of the experiments of Miller and M'Whorter ('14) on the origin of blood-vessels in the chick embryo. Further support is to be found in the more recent experimental evidence presented by Reagen ('15), which shows the origin *in loco* of vessels in isolated parts of chick embryos, and by Stockard ('15), which claims beyond doubt that in Fundulus embryos the heart endothelium and aorta arise *in loco* within the embryo, and here there are no vessels, nor even mesoderm, present on the yolk-sac in the cranial portion.

Fig. 6*a* represents the graphic reconstruction of the vascular system of the cranial portion of the Stage II. (*a*) ferret embryo. In this specimen the heart rudiment is represented merely by a transverse blood channel which lies across the median plane and unites the cranial ends of the two vitelline veins. The pleuro-pericardial cavity, together with the pleuro-pericardial canals, has already been described as having the shape of an inverted U-shaped canal which lies dorsal to the vitelline vein and the heart rudiment. Two rudimentary dorsal aortæ can be made out in this specimen. They run caudo-cranially one on each side of the medullary groove. They are still more or less plexiform in character, and they terminate blindly

at their cranial extremities. The absence of the first aortic arch, which is so conspicuously seen in the next stage, deserves particular notice. It is clear that at this stage of development in the ferret, the heart rudiment and the caudal part of the dorsal aorta are present, but the connection, *i.e.* the cranial dorsal aorta, the first aortic arch, and the conus arteriosus, between the heart and the caudal dorsal aorta, is still wanting (fig. 6*a*). A stage further in the development of the cranial portion of the dorsal aorta is illustrated by the Stage III. embryo (fig. 18). Here the dorsal aorta is seen to have established its connection with the heart rudiment through the first aortic arch. But exactly how this connection takes place, there is no evidence from which to form any definite conclusion. It is as yet impossible to decide whether the first aortic arch and the conus arteriosus when developed, as seen in the specimen just referred to, should be attributed to the result of a cranialward growth from the dorsal aorta, or as the direct outcome of an extension of the heart rudiment growing round the cranial end of the fore-gut to join the dorsal aorta and to constitute the conus arteriosus and the first aortic arch. All that can be said is that probably coinciding with the formation of the head fold the two dorsal aortæ are carried, *pari passu*, cranialward over the cranial end of the fore-gut, and possibly, as the result of a further growth from the blind ends of the aortæ towards the heart rudiment, these structures establish their communications with the heart. If this contention represents precisely what really takes place in the ferret embryo, the conus arteriosus and the first aortic arch must be considered as being the result of a further growth from the dorsal aorta. But if the other theory is to be accepted, that is, that the development of the conus arteriosus and the first arch is due to an extension of the heart growing round the fore-gut, then the development of these parts of the vascular system does not conform with the statement made by Bremer ('12) relating to the early development of the blood-vessels in the rabbit embryo of 5 somites. This investigator asserts that the dorsal aorta, the first aortic arch, the conus arteriosus, and the lateral heart are all parts of an original network of angioblast cords derived from the extra-embryonic plexus of blood-vessels. Another mode of origin which cannot, however, be overlooked, is that, after the heart rudiment and the dorsal aorta have been laid down, the remaining parts of the main vascular system of the cranial region of the embryo may develop *in situ* from the mesoderm. The view that parts of the intra-embryonic vascular system arise *in situ* cannot be ignored, for there is an overwhelming accumulation of conclusive evidence to indicate that the formation of the intra-embryonic blood-vessels is much more extensive and important than has hitherto been supposed.

From whichever point of view the development of the dorsal aorta, the first arch, the conus arteriosus, and the heart is to be looked upon, the fact remains that these structures do not develop simultaneously. This is clearly shown in fig. 1*a*, in which the heart rudiment and the dorsal aorta at this stage of development are all represented, yet there is nothing to indicate or to represent the future first aortic arch and the conus arteriosus.

It is certain that, in the ferret, mesoderm is laid down in the whole of the embryonic area before any blood-vessels appear in the area. It is also certain that some of the splanchnic mesoderm cells arrange themselves into an anastomosing plexus of larger and smaller strands. One of the larger strands lies lateral to the notochord on each side and ultimately is transformed into the dorsal aorta, whilst previously a strand along the anterior border of the area is transformed into the channel of communication between the vitelline vein of opposite sides.

The dorsal aorta and the transverse communication between the vitelline veins are at first quite separate from one another, except that they are both connected with the surrounding splanchnic mesoderm.

As the head fold develops the dorsal aorta and the transverse channel between the vitelline veins become united and the first aortic arches are formed. How the union occurs is not clearly shown by the specimens, for intermediate stages are wanting. It might be by growth caudalwards from the vitelline veins, or cranialwards from the aortæ, but it is more probable that arches of communication are formed *in situ* from the mesoderm, and that the whole process of blood-vessel formation in the embryo is one of transformation of cords of splanchnic mesodermal cells into tubes. The transformation takes place first in the anterior and posterior ends of the embryonic area, but extends more rapidly forwards than backwards, hence the dorsal aortæ grow from behind forwards and the last formed parts of the great vessels are the aortic arches.

Development of the Human Vascular System.

Some points in the early development of the human vascular system may now be discussed, although I have only had the opportunity of examining two very young specimens. According to Evans ('12), it is certain that in man, long before any vascular rudiments are found in the body of the embryo, and at a time before any mesodermic somites are formed, typical vascular rudiments are detected irregularly scattered, at first, over the surface of the ventral pole of the yolk-sac only, but on account of its comparatively small size the vascularisation of the whole surface of the yolk-sac is soon completed.

It is generally believed that, as in other vertebrates already studied,

these vascular rudiments make their appearance as nodular swellings of that part of the wall of the yolk-sac known as the area vasculosa, and are cell clumps lying between the mesoderm and the entoderm. It is claimed also that very shortly after their appearance, the peripheral cells of these cell clumps arrange themselves to form endothelium while the central ones remain as blood-cells.

In young human embryos it has been possible to demonstrate that, at a period before any vascular rudiments on the yolk-sac proper can be distinguished, there develop in the belly-stalk and chorion of the embryo indisputable blood-vessels which appear, at first, as strands of spindle cells possessing a lumen. This has been described by Fetzer ('10), and also observed by Graf Spee ('96) in the embryo Von Herff of ·37 mm. Others (Jung ('07) and Herzog ('09)) have called attention to the aggregations of endothelial cells in the belly-stalk. True blood islands in the belly-stalk near the allantois have been described also by Grosser ('13) and Debeyre ('12). Frassi ('08) also is in favour of the view that well-formed angioblastic cords can be detected on the ventral surface of the yolk-sac and in the belly-stalk and chorion.

I have examined very carefully the whole series of sections of "A very early human ovum embedded in the uterus" described by Johnstone ('14), and have found that true vascular endothelium in the form of isolated cords is present in the ventral pole of both of the twin vesicles near their attachments to the blastocysts. Dr Johnstone, however, considers these endothelial cords as merely localised thickenings which he was unable to denote definitely as the precursors of vessels.

Judged in the light of observations made by other investigators, it is not unreasonable to look upon what have been considered as the "mere localised thickenings" by Dr Johnstone as in reality true vascular endothelial cords. The reason for this belief is the fact that, in position and in their general characters, the cell cords or "thickenings" in question bear a close resemblance to those which have been described in other early human embryos as endothelium by Fetzer, Graf Spee, Jung, Frassi, and others.

Recently Bremer ('14) has stated that, in human embryos, the earliest blood-vessels appear separately in the yolk-sac and in the belly-stalk in the form of multiple rudiments which are for the greater part funnel-shaped invaginations of the surface of the mesoderm. By a partial fusion of the walls of an ingrowth, a portion of the cœlom, bordered by mesoderm, may be cut off as a separate cavity, lying deep within the substance of the belly-stalk. This investigator, therefore, believes that the endothelium arises either by delamination from the walls of such a detached portion of

the cœlom, or by direct extension, in the form of an angioblastic cord, from the mesothelial ingrowth.

Most authors believe that the early development of the vascular rudiments in the belly-stalk and chorion in human embryos happens before the yolk-sac proper exhibits any vascular elements. That this should be the case is due to the fact that in human embryos the vitelline circulation is of secondary importance. The belly-stalk and chorion, on the other hand, constitute the primary connection between the embryo and the placenta, and are therefore the first to be vascularised. This deviation from the ordinary type of development is but one of the remarkable series of variations with which man is distinguished from his fellow-creatures.

All facts, therefore, tend to point that in man the first vascular endothelium is laid down in the belly-stalk and chorion. This furnishes an additional evidence in favour of the biphyletic origin of blood-cells and blood-vessels. The next question to be considered is whether the vascularisation of the yolk-sac proper is to be regarded as the extension of a further growth from the vascular rudiments in the belly-stalk and chorion, or whether the process arises *in situ* by separate vascular rudiments. Bremer ('14) thinks that the vascularisation of the yolk-sac proper is a separate manifestation, but it is quite possible that the first vascular endothelium of the yolk-sac is the result of an extension from the endothelium of the belly-stalk and chorion. Unfortunately, Johnstone's specimen gives no definite indication either of the origin of the cell cords or of their extension.

Development of the Heart and Pericardium.

In the literature dealing with the development of the heart and pericardium, much has been written regarding the developmental processes of these structures in mammals, but in man much is required yet before a comprehensive knowledge of the developmental phenomena can be obtained. It is still a speculation if the earliest rudiment of the human heart is essentially similar to that of the mammalia. Tandler ('12) inclines to the belief that they are similar. It is not to be expected, at present, that the comparison of the development of the human heart with that of the mammalia will throw much light upon the subject until the various developmental processes of the different members of the mammalian embryos are first understood.

In mammals, as has been stated previously, the first rudiment of the heart is the appearance of a number of cells—the angioblast of His, which are distinguishable in embryos of 2–3 primitive somites. These vascular cells appear between the entoderm and mesoderm in the cranial region of

the embryo on each side not far from the median plane. They are responsible for the development of the endothelial heart tubes only, the remaining structures of the wall of the heart being derived from that part of the visceral cœlomic wall which has been designated by Mollier ('06) the heart-plate. It is generally believed that the first appearance of the vascular cells of the mammalian heart is bilateral and is located on the ventral aspect of the pleuro-pericardial canals. Hensen ('76) is credited as being the first who observed this bilateral origin of the heart. A fusion of the two endothelial tubes next takes place, and the paired heart rudiments are therefore transformed into an unpaired heart tube, but the precise mode of this transformation is, up to the present, *sub judice*.

As far as the bilateral origin of the heart rudiments is concerned there seems to be still a little doubt. In all vertebrates that have been investigated all writers incline to believe that the heart rudiments originate in two lateral parts, but precisely how these two parts are brought together to form an unpaired heart is much a disputed point.

As already pointed out (*vide supra*), some believe (*a*) that in mammals, as in birds, the two endothelial tubes, out of which the heart is formed, appear at a time when the lateral folds which are said to form the ventral wall of the throat are only just visible; (*b*) that, on the formation of the lateral folds of the splanchnic walls, the two halves of the heart, enclosed within the hitherto symmetrical and laterally placed pleuro-pericardial cavities, become carried medially and ventrally until they fuse on the ventral aspect of the fore-gut; and (*c*) that the heart is therefore provided, at least for a time, with a ventral and a dorsal mesocardium.

Professor Wilson of Sydney ('14), writing in favour of the presence of a ventral mesocardium in human embryos, asserts that the human heart, like the amphibian, has, at a certain period of development, a ventral mesocardium. This author bases his conclusion on the result of the examination of a series of sections of a human embryo measuring 1·78 mm. catalogued H3 in his series, which was aborted and is admittedly in an indifferent if not bad state of preservation. In addition it is stated that the specimen was cut "in a plane intended to be transverse to the long axis of the embryo, but which turned out to be distinctly oblique." The obliquity appears to have taken place in two planes instead of one, namely, a ventro-dorsal and a lateral. No reconstruction of the heart of the embryo has been made to verify his statement, and the number of somites has been hesitatingly determined to be three pairs.

In fig. vi. of Wilson's paper an incomplete "septum" in the pericardial cavity has been named by him the "septum proprium interpericardiacum." This he looks upon as evidence of the bilateral origin of

the pericardial cavity, which, according to his observation, ends on each side "blindly without establishing any communication with other cœlomic cavity such as occurs later, *e.g.* in Mall's embryo, No. 391." In the same figure the heart appears to have an attachment to the ventral wall of the pericardium which presumably Wilson calls the ventral mesocardium.

It is quite possible, as far as the figure shows, that the so-called septum proprium interpericardiacum is merely a fold of the pericardial wall which has never, at any time, formed a true septum. The statement made regarding the blind termination of the pericardial cavity on both sides of the embryo is contrary to all known facts established by other observers on this structure in mammals. The narrow communication between the pericardial cavity and the cœlomic cavity has probably been overlooked by Wilson in his specimen on account of the poor histological details of the sections, or the pleuro-pericardial canal might have been obliterated in such a way as to render the communication unrecognisable. If the observation of Wilson is the true interpretation of the condition of the pericardium at this stage of development, then the balance of evidence in favour of the primary communication of the pericardial cavity with the general cœlomic cavity in mammals is totally upset. But the unsatisfactory condition of the sections, from a histological point of view, unfortunately affords ground to doubt the accuracy of the observation, otherwise this embryo opens a new field for further investigations into the true nature of the pericardial cavity at this particular stage of development in the human embryo. The connection between the heart tube and the ventral wall of the pericardial cavity in Wilson's specimen can be feasibly explained in the following way. If the obliquity of the plane of section is such that it passes through the septum transversum as well as the heart tube situated immediately cranial to it, it will be seen that what appears to be the ventral mesocardium is really a part of the septum transversum. Moreover, it is quite possible that what Wilson considers to be the two endothelial tubes, may after all turn out to be the two vitelline veins passing through the septum transversum to reach the sinus venosus cranially, and that the specimen he has been dealing with might have been pathological.

I was fortunate enough to have at my disposal also the second young human embryo which has been described by Dr Johnstone ('14) in his "Contribution to the Study of the Early Human Ovum." When the sections came to my hand, it was found that the series was unfortunately not entirely complete; consequently a reconstruction of the heart of this interesting stage had to be abandoned. Nevertheless the series serves one particular purpose very well, namely, that it shows that this specimen has been cut in a plane not dissimilar to that of Wilson's embryo, and that the

heart tube in Dr Johnstone's specimen bears a close resemblance to that of Professor Wilson's specimen, in so far as the anatomical relationships of the heart are concerned.

Though no description of the heart of the embryo has been made by Dr Johnstone in his paper, a few very interesting points can be detected by an examination of the serial sections. At first glance the section of Johnstone's specimen, from which fig. 35 is taken, appears to indicate that the heart has a ventral mesocardium connecting the ventral part of the heart tube with the ventral wall of the pericardium. But on closer examination, what seems to be ventral mesocardium is found to be really

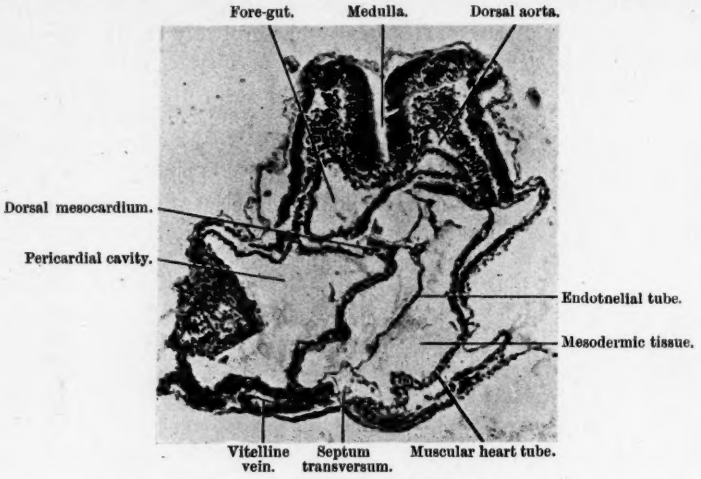


FIG. 35.—Human embryo. ×100.

part of the septum transversum, for when this structure is traced forwards and backwards in the series, it is found that the vitelline veins traverse it to join the sinus venosus. Fig. 36 shows that the vitelline vein passes through the septum transversum to reach the heart. Cranially to this there is nothing to indicate a ventral mesocardium, the cavity of the pericardium extending without interruption from side to side (fig. 37) Professor Robinson has very kindly looked through the sections of Dr Johnstone's specimen with me and has confirmed the above statement.

In the chick, on the other hand, a ventral mesocardium is recognisable, but this is due, as Robinson ('02) points out, to the relatively late penetration of the pleuro-pericardial canals into the mesoderm in the cranial region. The pleuro-pericardial canals do not extend round and unite in front of

the medullary plate in early stages, but only at a later stage do they penetrate into the floor of the fore-gut after the mesoderm has been

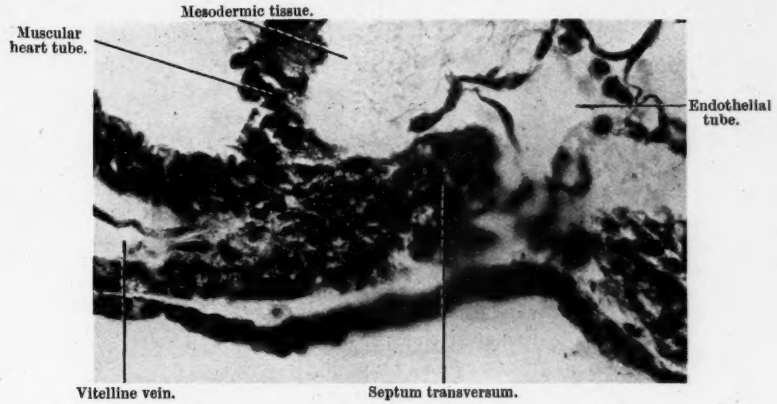


FIG. 36.—Septum transversum in fig. 35 magnified. ×500.

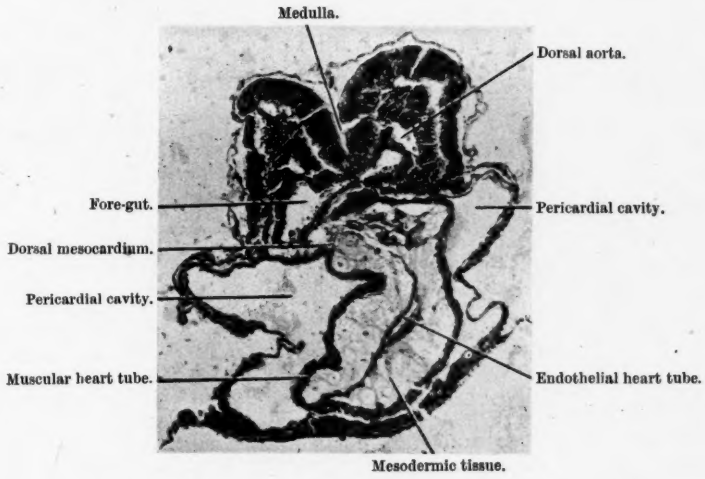


FIG. 37.—Human embryo. ×100.

formed. The lateral cavities therefore do not at once become continuous, but remain separated from each other by a double layer of mesoderm which constitutes the ventral mesocardium.

According to Robinson ('02) the pericardial mesoderm appears in the pericardial portion of the embryonic area, and it is there completely differentiated into somatic and splanchnic layers before the head bend is developed; there is, therefore, a single pericardial cavity to begin with, which extends from side to side along the cranial boundary of the embryonic area. As the head bend develops, the single pericardial cavity is reversed, and it is carried into the ventral wall of the fore-gut, where it forms a U-shaped tube which communicates at each end with the general cœlom. The heart rudiments are formed in the splanchnic layer of the pericardial mesoderm; therefore, after the reversal of the area, they lie in the dorsal wall of the pericardial cavity attached only by a dorsal mesocardium to the ventral wall of the fore-gut, but they are never, at any time, connected with the ventral wall of the pericardium by a ventral mesocardium.

Rouvière ('04), whilst agreeing with Robinson as to the absence of the ventral mesocardium, describes the formation of the lateral pleuro-pericardial canals which grow cranially round the cranial end of the brain-plate and fuse to form a continuous channel. Miss Parker ('15), in her investigation into the early stages in the development of Marsupials, modifies Rouvière's opinion, saying "that while the initiation of head-fold formation is in all probability due to the forward growth of the brain-plate, there occurs also an active backward growth of the anterior intestinal portal (umbilical orifice). This process is associated with the rapid expansion of the pericardium which occurs at this period of development, and which brings about the backward and inward growth of the layer of splanchnopleure limiting the pericardium."

Against the view that a backward growth occurs in the cranial margin of the umbilical orifice is the contention of Robinson ('02) that "the orifice (of the umbilicus) is not reduced in size during the early stages of development by the convergence of its margins towards a central point. This being the case, no tucking off of the embryo from the surface of the ovum can occur; on the contrary, what does occur is almost the exact opposite of such a process, for the margin of the area remains as a relatively slow-growing region, whilst the embryonic and extra-embryonic portions of the wall of the ovum rapidly increase in extent. Under these circumstances, it follows that the margin of the embryonic area will soon appear as a ring between the upper or embryonic, and the lower or extra-embryonic parts of the ovum, both of which have expanded beyond it in all directions."

The evidence afforded by the ferret material I have described shows that there is no ventral mesocardium in the ferret, and all the indications it gives are strongly opposed to the idea that any part of the gut closure is affected by the fusion of the lateral folds.

In the Stage II. (*a*) and (*b*), in which the head fold of the ferret embryo has not yet appeared (figs. 6*a* and *b*, 11*a* and *b*), the pleuro-pericardial cavity is present in the median plane, and immediately caudal and ventral to this the two vitelline veins communicate with one another across the median plane. There is no evidence that they were even separate from one another, but the union may be called the primary union of the heart rudiments; it should be specially noted that the term "primary" proposed signifies that the right and left parts separate from one another and are again fused by a "secondary" union. To this point reference will be made subsequently in connection with the discussion of the formation of the unpaired heart rudiment from the two separate endothelial tubes.

At Stage II. of development the separation of the right and left parts of the rudimentary heart has commenced, and the pleuro-pericardial cavity and the heart rudiments are all represented before there is any indication of the formation of the fore-gut or the head fold (fig. 6*a*). It should also be noticed that when the heart rudiments and the pleuro-pericardial cavity first make their appearance, the former invariably lie ventral to the latter (figs. 6*b* and 8). In the subsequent stages of development (Stage III. and onwards) a change takes place in their position, with the result that the heart rudiments occupy a plane dorsal to the pleuro-pericardial cavity, and are connected with the ventral aspect of the fore-gut only by the reflection of the splanchnic wall of the pleuro-pericardial cavity. The reversion of positions of the heart and the pleuro-pericardial cavity can only be explained, as suggested by Professor Robinson ('02), by a forward growth of the head fold to form the fore-gut with the cranial margin of the umbilical orifice remaining stationary. With the development of the head fold the heart rudiments suffer a rotation round a transverse axis over the pleuro-pericardial cavity. Consequently when the two heart rudiments which became separated are again brought together to form one endothelial tube, it is connected with the ventral surface of the fore-gut only by a dorsal mesocardium, which is formed by the reflection of the splanchnic layer of the pleuro-pericardial cavity over the lateral and ventral surfaces of the two heart tubes; the portion of the splanchnic wall of the pleuro-pericardial cavity in which the endothelial tube lies is in the meantime pushed ventrally, and thus the dorsal mesocardium is elongated. There is no indication of a ventral mesocardium.

Since the time of Hensen ('76), the first appearance of the heart rudiments has been considered to be bilateral, that is to say, the heart rudiments develop as two separate endothelial tubes, one on each side of the embryo not far from the median plane and on the ventral aspect of the pleuro-pericardial canals. Recently the bilateral endothelial tubes have been

traced to the stage of angioblastic cords, which have also been described as lying between the mesoderm and the entoderm. Spaces soon make their appearance in the vascular masses, and when these coalesce, two endothelial tubes are thus formed, one on each side of the embryo, ventral to the pleuro-pericardial channels. In the ferret the coalescence of the vascular endothelium is to produce one endothelial tube (the "primary" union of the heart rudiments) lying across the median plane caudo-ventral to the pleuro-pericardial cavity (Stage II. (*a*), figs. 6*a* and *b*). This occurs, it should be remembered, at a time before the formation of the fore-gut has made its appearance. When this "primary" endothelial tube is traced laterally, it is found to communicate with the two vitelline veins (fig. 6*a*). A search through the literature on the early stages of development of the mammalian heart has failed to discover any account of this "primary" union of the heart rudiments. Miss Parker, in the course of her investigation into the early stages in the development of Marsupials, notices the early or "primary" union of the heart rudiments across the median plane in Stage II. *Dasyurus viverrinus* (8·5 mm.); its significance, however, has not been explained by her.

That the "primary" union of the heart rudiments to form a single endothelial tube is not a singular occurrence due to any abnormal or pathological conditions, and that this stage of development of the heart is an important one is proved by the fact that a similar phenomenon repeats itself in another ferret embryo (Stage II. (*b*), figs. 11*a*, *b*, and 12*a*, *b*, *c*), in which the heart and the pleuro-pericardial cavity exhibit features similar to those observed in the Stage II. (*a*) ferret embryo. It has to be emphasised once more that the "primary" union of the heart rudiments across the median plane as a transverse vascular channel lying caudo-ventral to the pleuro-pericardial cavity occurs at a period before any indication of the head fold or the formation of the fore-gut can be detected.

The next stage of development of the heart in the ferret embryo is represented by the 2·3-mm. embryo (Stage III.). In this specimen, which is obviously slightly older than the Stage II. (*a*) and (*b*), the medial part of the "primary" endothelial tube shows indications of splitting into two lateral endothelial tubes, for two non-vascular loculi divide its central portion incompletely into a cranial and a caudal portion (fig. 18). Apparently the destruction of the central part of the rudimentary transverse heart ("primary" union) proceeds still further as development goes on, until it is completely separated into a right and a left half; for in the Stage IV. ferret embryo the heart rudiments are represented there by two separate longitudinal endothelial tubes lying side by side close together (fig. 27). It is again to be noted that the head fold and the fore-gut of

this ferret embryo (Stage III.) have already begun to develop, since at the cranial end two vessels, one on each side of the median plane, run cranially from the heart rudiment. They arch round the cranial end of the fore-gut and form the first pair of aortic arches, which terminate dorsally in the corresponding dorsal aorta (fig. 18).

In the comparison of this stage of development of the heart in the ferret with that of other mammals of a similar stage of development, the Stage III. *Perameles nasuta* (1 S) of Miss Parker may be cited; the total length of her specimen, after partial flattening under cover glass, from the anterior margin of the brain-plate to the hinder extremity of the primitive streak is, according to Miss Parker, 7·5 mm. In her specimen two endothelial tubes are depicted lying side by side in the pleuro-pericardial cavity. Cranially each endothelial tube becomes continuous with the ventral aorta, which runs underneath the ventral surface of the fore-gut. As the cranial extremity of the fore-gut is reached, the ventral aorta bends dorsally round the blind end of the fore-gut and communicates with the dorsal aorta, so forming the first aortic arch. Whilst still in the pleuro-pericardial cavity the heart tube is described as giving off a lateral branch which is presumably the second aortic arch. What is most striking and interesting in Miss Parker's specimen is, that "in the median space between the anterior ends of the endothelial heart tubes, are a number of scattered angioblast cells lying between the splanchnic mesoderm and the entoderm." Miss Parker believes that these cells possibly represent the primordia of the capillaries and afford an instance of the origin of angioblast cells from the splanchnic mesoderm after the establishment of the definite endothelial heart tubes. Judging from what has been observed in the ferret embryo of Stage III., it is perhaps more correct to interpret these angioblast cells as being the remains of the once "primary" union of the heart rudiments. This "primary" union is well developed in the ferret embryo of Stage II. (*a*) and (*b*), and also in the Stage II. *Dasyurus viverrinus* (8·5 mm. A) of Miss Parker. The explanation for the breaking up of the "primary" union of the heart rudiments to form two separate endothelial tubes is, however, not apparent in the light of our present knowledge of the development of the mammalian heart. It is conceivable that partly as a result of the development of the fore-gut cranialward, in the manner pointed out by Robinson ('02), and partly also due to the rotatory movement of the heart rudiments from a position ventral to the pleuro-pericardial cavity to a position dorsal to it round a transverse axis, the cross channel, that is, the "primary" union of the heart rudiments is, at first, put on the stretch, and finally separated into two endothelial tubes lying side by side, each of which becomes continuous with its corresponding dorsal aorta through the

conus arteriosus and the first aortic arch. In the ferret embryo of Stage III. (fig. 18) the connection between the heart and the dorsal aorta has already established itself before the heart (after its "primary" union) has again completely separated into two halves. In the case of the Stage II. Dasyurus of Miss Parker, the "primary" union of the heart rudiments is described as giving rise to the first aortic arch, which follows the antero-lateral margin of the gut almost to the median plane and there becomes continuous with the corresponding dorsal aorta. But what has been taken for the first aortic arch by Miss Parker may, after all, prove to be the plexus between the dorsal aorta and the vitelline vein, which has been observed by Bremer ('12) in the 3·4-mm. rabbit embryo.

It will be noticed, then, there is evidence to show that, at a period before the formation of the fore-gut, the first rudiment of the heart in the ferret is single and is situated in the median plane of the embryo, caudo-ventral to the pleuro-pericardial tube cavity, in the form of a transverse endothelial tube which is destitute of any blood-cells. Laterally it is in direct communication with the two vitelline veins, one on each side of the embryo. But exactly how this "primary" transverse heart tube is formed it is impossible to make any definite statement. The contention of His ('00) does not fully account for the origin of this "primary" union of the two vitelline veins, for, according to His ('00), two endothelial tubes are directly formed from the ingrowth of the two vitelline veins which, by a further growth, communicate with the two dorsal aortæ. Possibly the "primary" union of the heart rudiments is the result of an ingrowth from the vitelline veins which, instead of linking up each with its corresponding dorsal aorta, as His would have imagined, have grown across the median plane. In this way the U-shaped vitelline system is, at least for a time, not connected with the longitudinal aortic system cranially. This is exactly what is seen in the ferret embryo of Stage II. (*a*) (fig. 6*a*). It is also possible, and perhaps more probable, that the "primary" union arises *in situ* and is afterwards joined to the two vitelline veins.

From whatever point of view the development of the heart is looked upon, it is clear that in the ferret the first rudiment of the heart appears as a cross channel situated ventro-caudally to the pleuro-pericardial cavity, and is connected only with the venous system, which is composed of the two vitelline veins laterally. The arterial system, that is, the dorsal aortæ, remains, at least for a time, distinct and unconnected with the heart rudiment. No explanation can at present be offered as to why the heart rudiment, when first represented, should only be united with the venous circulation. It is evident that further light in this field of investigation is required before a solution can be obtained.

Quite recently Professors Robinson and Gibson ('16), in their description of a reconstruction model of a horse embryo twenty-one days old, mention that "the allantoic blood-vessels consist of a number of dilated capillaries which form a coarse network on each side. Each lateral network receives two branches from the caudal end of the dorsal aorta of the same side, and it terminates, at the caudal end of the allantoic mass, in a terminal transverse sinus from which the umbilical veins take their origin. But, in addition to the connection with both umbilical veins through the terminal sinus, each vascular network also communicates directly with the umbilical vein of the same side." The terminal transverse sinus at the caudal end of the allantoic mass of the horse and the transverse heart rudiment situated in the cranial end of the ferret embryo may together represent at one time a portion of an original complete ring of circulation.

The next phase of development of the heart is represented by the separation of the "primary" heart rudiment into two distinct endothelial tubes lying closely together, one on each side of the embryo, not far from the median plane (Stage IV.). Coinciding with the development of the heart, the head fold appears, and as the formation of the fore-gut proceeds, the heart rudiment suffers a reversion with regard to its relation with the pericardium, for it is seen that when the fore-gut is formed the heart is found on the dorsal aspect of the pleuro-pericardial cavity and is attached to the ventral surface of the fore-gut.

Each tube is covered by the splanchnic wall of the pleuro-pericardial cavity on its lateral, ventral, and medial surfaces. Dorsally they are connected with the ventral aspect of the fore-gut by the reflection of the wall of the pleuro-pericardial cavity. Ventrally the pleuro-pericardial cavity passes from side to side (fig. 27). It is to be noted that the two tubes lie far apart from each other cranially and caudally where they emerge from the pleuro-pericardial cavity. The distance between them is greater caudally (fig. 26) than cranially (figs. 27 and 28*d*). It is obvious that at a stage further, when the two heart rudiments are brought together to form one endothelial tube, it is connected only with the ventral surface of the fore-gut by a dorsal mesocardium and no ventral mesocardium can possibly be developed.

Cranially each endothelial tube can be traced to its corresponding dorsal aorta through the first aortic arch, and caudally each tube communicates with its corresponding vitelline vein in the region of the septum transversum (figs. 21, 25, and 27).

It is generally held that the rate of growth of the two endothelial tubes exceeds that of the pleuro-pericardial cavity. Consequently, as the result of the different rate of growth, the two tubes, instead of having a

straight appearance, are thrown into loops before the "secondary" union takes place.

Miss Parker ('15) thinks, however, that at this stage of development the pericardium grows rapidly in length and decreases in width so that the heart tubes are brought together by longitudinal stretching of that part of the pericardial wall which lies between them. In the ferret it is clear that this is not the case; the two endothelial tubes seem to grow more rapidly in length than the pericardium, with the result that loops are formed with constrictions here and there to mark out the different subdivisions of the heart (atrium, ventricle, bulbus, etc.), before any fusion of the two tubes takes place (Stage IV. fig. 27), these subdivisions appear to remain even when the two endothelial tubes have partially united (Stage V. fig. 31). The appearance of these loops in the endothelial tubes speaks against the theory of stretching advanced by Miss Parker. For, if it were true, the result of any stretching of that part of the pleuro-pericardial wall which lies between the medial borders of the two endothelial tubes would, in the first instance, be the undoing of the loops, or the prevention of their formation, before any approximation of these tubes could be effected.

In the ferret (Stage IV.) what has really happened is this, that as the result of the rapid growth, the two endothelial tubes are thrown into loops, and as the result of a further growth of the two tubes medially towards each other, the part of the pleuro-pericardial wall which lies between them is pushed ventrally. When fusion of the two endothelial tubes takes place, the unpaired heart is, therefore, attached only to the ventral wall of the fore-gut by the dorsal mesocardium. Ventrally the splanchnic wall of the pleuro-pericardial cavity passes from side to side across the ventral aspect of the fused heart tube, there being no fusion of this part of the pleuro-pericardial wall, as supposed by Miss Parker.

Asymmetry of the heart tubes, either before or after fusion takes place, has been noted in the ferret embryos (Stages IV. and V., figs. 27 and 31), as in the Stage IV. *Perameles nasuta* and also, in a measure, in the Stage V. *Perameles obesula* (10, viii., '03) of Miss Parker and likewise in the 5·7-mm. dog embryo of Bonnet ('01). There seems to be a tendency for the two endothelial tubes, even before fusion, to curve and to be shifted distinctly as a whole to the right side with the concavity of the bend facing the left. In Stage V. (fig. 31) the fusion of the two endothelial tubes in the ferret takes place in the ventricular region, and the fused part lies clearly on the right side of the median plane. The fact of this occurrence contradicts, in a very convincing manner, the theory of stretching of the pleuro-pericardial wall, for the fused portion of the two endothelial

tubes should occupy the median plane of the embryo if the two tubes were really brought together by the uniform stretching of that part of the splanchnic wall of the pleuro-pericardial cavity which lies between them. There is no evidence to prove that the fusion of the two tubes, occurring on the right side, may be due to an uneven stretching of the dorsal wall of the pleuro-pericardial cavity.

In the Stage IV. *Perameles nasuta* (2 P) of Miss Parker the description of the heart in the text does not seem to agree with her illustration—Plate 1, fig. 5. In the text it is stated: "They (the two endothelial tubes) have fused at their cephalic extremity, the fused portion extending through some eighteen sections and representing the most closely approximating portions of the endothelial tubes. . . . From it is derived the bulbus (conus) arteriosus. . . . Posterior to this fused portion, the endothelial tubes lie close together but unfused for a considerable portion of their length and then diverge widely and pass into the vitelline veins." In her illustration, on the other hand, it appears that the fused portion represents really more than the conus arteriosus. Possibly the ventricles also have fused across, because in the figure it shows that at least the cranial half, if not more, of the two endothelial tubes have fused. If this is the case, it is difficult to explain why in the next stage of development (Stage V. *Perameles obesula* (10, viii., '03) of Miss Parker) the bulbus is the only portion of the heart in which the endothelial tubes have actually fused, and the ventricles have become once more separated.

In the text and the figures illustrating Stage IV. *Perameles nasuta* (2 P) and Stage V. *Perameles obesula* (10, viii., '03) of Miss Parker, there are no data to be found upon which the magnification and length of the embryos in question can be gauged. But as far as one can judge from the illustrations alone, the figures of Stage V. *Perameles obesula* are undoubtedly of a higher magnification although probably taken from an embryo of a greater length than that of the Stage IV. *Perameles nasuta*. If it is so, an explanation is needed to account for the decrease in length of the fused portion of the two endothelial tubes seen in Stage V. It is unfortunate that these important data should have been omitted by Miss Parker in her paper, for their absence diminishes the value of her communication when an attempt is made to use it for the purpose of solving the points under consideration.

Hitherto the heart tube with its time-honoured S-shaped character has been the subject of much dissertation. The literature on the development of the S-shaped heart rudiment is so voluminous and confusing that only a brief summary on this subject can be given. All writers have laid great stress on the subsequent development of the fused endothelial tube which

is now covered with its myocardial coat. It is generally believed that the next phase of development of the fused heart tube, consisting as it does of an inner endothelial tube and an outer myocardial covering, is the acquisition of the well-known S-shaped form. The caudal portion of the single heart tube grows cranio-dorsally and to the left to form the atrial limb, and the cranial portion grows caudo-ventrally and to the right to form the ventricular limb. In the Stage IV. ferret embryo model (fig. 22), it has been shown that the external configuration of the muscular wall of the heart does not necessarily furnish a true index to the condition of the development of the enclosed endothelial tubes, for it has been remarked upon that although the muscular coat of the heart rudiment may have acquired the familiar S-shaped appearance, yet the two endothelial tubes have not begun to fuse. Moreover, the segments exhibited in the muscular tube do not correspond in the least with the dilatations and constrictions of the underlying endothelial tubes. Furthermore, in the dog, it has been pointed out by Bonnet, and in Marsupials by Miss Parker, that primary divisions of the endothelial tubes into sinus venosus, atrium, and ventricle occur before they have completely fused to form a single tube. Similar divisions of the heart tubes are present also in the Stage IV. ferret embryo (*vide supra*). These facts therefore show that the primary divisions of the heart rudiment take place in the endothelial tubes at a time when no fusion can be detected, and that the convolutions of the S-shaped muscular coat of the heart do not necessarily represent the different segments of the underlying endothelial tubes.

In connection with the fusion of the two endothelial tubes there is one more point which requires attention. Many investigators have noted the asymmetry of the heart rudiments at this period of development. Deviation of the two heart tubes to the right, before and after fusion, has also been observed in the mammalian heart. In the ferret these features are present. The significance of the asymmetry and deviation of the two endothelial tubes have, so far, not been fully explained by those who have made these observations. It has been noted that the ventricular portion of the heart is the first to fuse, and is situated on the right side of the embryo (Stage V. fig. 31). The fused portion in fact represents the junction between the ventricular and the atrial limbs of the future S-shaped heart tube. As fusion proceeds cranially and caudally, more parts of the heart tubes are taken in to form the two limbs of the S-shaped heart rudiment until the two tubes are completely fused. The result of this fusion is to produce a ventricular limb which is situated ventrally and to the right side and an atrial limb which is directed dorsally and to the left.

It should also be remembered that in the space between the myo-

cardium and the endothelium of the heart tubes there is a more or less thick mass of loose mesodermic tissue which separates not only the former from the latter but also the two endothelial tubes from one another before their fusion (Stage IV. figs. 27 and 28*a*, *b*, *c*). This mass of loose tissue, though playing an important role in the establishment of the sino-ventricular bundle (Mall ('12)) in the subsequent development of the heart, is essentially a passive element at this stage of development. It permits, on the one hand, the growing endothelial tubes to assume their various bendings, constrictions, and dilatations independently, and adapts itself, on the other hand, to the characteristic curling of the muscular tube into an S-shaped appearance. This point is clearly shown in the Stage IV. ferret embryo in which the two endothelial tubes have, as already noted, differentiated into their various divisions in advance of their fusion (fig. 27), whilst the muscular wall of the heart has seemingly acquired the familiar S-shaped form (fig. 22).

It is obvious, therefore, that owing to the interposition of this more or less thick mass of mesodermic tissue, the endothelial tubes do not follow, in a faithful manner, the various curvatures and bulges of the myocardial covering of the heart, and it would be a mistake to try to determine, at this stage of development, the true nature of the two endothelial tubes by the simple examination of the condition and shape of the muscular coat, without ascertaining, at the same time, the various features of the underlying endothelial tubes and comparing these with those exhibited by the muscular covering.

It may therefore be concluded that, at least, from the first appearance of the paired heart rudiments as two endothelial tubes to the time of their "secondary" fusion, the myocardium has little or no common relationship with the underlying endothelium; that the two structures are quite independent of each other, as far as their individual growth is concerned; that the various constrictions and dilatations of the two endothelial tubes have a definite significance; that these constrictions and dilatations foreshadow the site and limits of the future sinus venosus, sino-atrial canal, atrium, atrio-ventricular canal, ventricle, and bulbus cordis; and that the muscular tube comes into conformity only at a later period.

Summary and Conclusions.

A. *The Blood Cells and Vessels.*

Hitherto it has been the general belief that blood-cells and vascular endothelium in mammals are derived from a common origin which, according to some, is mesodermic, and others, entodermic, and that, whichever

may be the source of origin, the vascular rudiment appears, at first, as angioblastic cells lying between the mesoderm and entoderm. It has been claimed also that the peripheral part of the angioblast soon resolves itself into an uninterrupted network of endothelium, and the central part into clusters of blood-cells. It has been stated further that the endothelium so formed is capable of giving rise to new blood-cells.

The facts revealed by the study of the early stages in the development of the ferret point to the conclusion that, whilst blood-cells and vascular endothelium are closely related to each other and are found invariably between the mesoderm and entoderm, there is evidence to show that, in the ferret, the origins of these two vascular elements are separate and distinct—the blood-cells arising from the entoderm and the vascular endothelium from the mesoderm.

Blood-cells develop first extra-embryonically in the area vasculosa in the form of clusters of spheroidal cells which are provided with large and round nuclei and with a comparatively small amount of protoplasm. These are for the most part found adherent to the entoderm in the neighbourhood of their origin before they are engulfed by the endothelium, and are, in most instances, identical in structure with the entodermal cells where the contact is intimate.

On the other hand, the cells which form the endothelial rudiment are mesodermic in origin and are, without exceptions, spindle or flattened in shape. They are generally connected with one another by long slender protoplasmic processes, the result of which is to form a network of endothelium. This network is capable of extension by buddings which grow either into the embryo or on to the yolk-sac. The blood-cells are next engulfed by the vascular endothelium which grow round them, and in this way they are taken into the circulation.

B. *The Intra-Embryonic Blood-Vessels.*

The caudal portion of the dorsal aorta communicates, at a very early stage of development, with the yolk-sac circulation through the vitelline arterial plexus. Cranially the dorsal aorta stops short and remains unconnected with the heart rudiment as long as there is no head fold or fore-gut. This part of the dorsal aorta makes its appearance in association with the development of the head fold and fore-gut.

The conus arteriosus and the first aortic arch develop after the "primary" heart rudiment, the two vitelline veins, and the dorsal aortæ are all represented, and at the time when the formation of the head fold and fore-gut has begun.

The vitelline veins are two in number, one on each side of the embryo.

They lie for the greater part of their extent ventro-medial to the pleuro-pericardial canals. They grow from the wall of the yolk-sac into the cranial extremity of the embryo. They are, at an early period, united across the median plane to form the "primary" heart rudiment which lies between the pleuro-pericardial cavity dorso-cranially and the bucco-pharyngeal membrane caudally. A short distance caudal to the "primary" heart rudiment, each vitelline vein sends out offshoots medially to anastomose with the cranial end of its corresponding dorsal aorta.

C. *The Pericardium and the Heart.*

Before there is any indication of the head fold or the formation of the fore-gut, the pleuro-pericardial canals have grown across the median plane of the cranial end of the embryo to form the pleuro-pericardial cavity which, in relation with the "primary" heart rudiment, lies cranio-dorsal to it. As the head fold and fore-gut develop by growing cranially, a rotation of the pleuro-pericardial cavity and the heart rudiment round a transverse axis takes place, with the result that the former occupies a position ventral to the latter and the "primary" heart rudiment is now found ventral to the fore-gut.

In the subsequent stages of development the "primary" heart rudiment divides into two endothelial tubes, each of which is covered laterally, ventrally, and medially by the splanchnic wall of the pleuro-pericardial cavity and is attached only dorsally with the ventral aspect of the fore-gut by the reflection of the pleuro-pericardial wall. As a result of the growth of the two endothelial tubes towards the median plane, the part of the splanchnic wall of the pleuro-pericardial wall which lies between them is thereby pushed ventrally. When fusion of the two endothelial tubes occurs, the "secondary" heart tube is consequently attached only dorsally to the ventral surface of the fore-gut by the dorsal mesocardium. Ventrally there is no fusion of the pleuro-pericardial wall, and therefore no ventral mesocardium can possibly be developed.

At an early period when the pleuro-pericardial cavity has not yet reversed its position, and when there is no indication of the formation of the head fold or the fore-gut, the heart rudiment appears as a transverse blood channel—the "primary" heart rudiment—situated in the median plane ventro-caudal to the pleuro-pericardial cavity and cranial to the bucco-pharyngeal membrane. Laterally the "primary" single heart rudiment communicates with the two vitelline veins, one on each side of the embryo. At this stage of development the cranial extremities of the two dorsal aortæ are found, for a considerable distance, caudal to the heart rudiment.

In the subsequent development of the embryo when the head fold and the fore-gut make their appearance by growing cranially, the pleuro-pericardial cavity and the "primary" heart rudiment undergo a rotation round a transverse axis, with the result that their positions are reversed, so that the heart rudiment now lies dorsal to the pleuro-pericardial cavity.

The division of the "primary" single transverse heart rudiment into two longitudinal endothelial tubes is due to the fact that, at this period, the fore-gut grows rapidly cranially in length and ventrally in width, together with the expansion of the pleuro-pericardial cavity in all directions, so that the transverse heart rudiment which lies between these structures is at first put on the stretch, and is subsequently divided across into two endothelial tubes, a right and a left. Concurrently with the development of the head fold and the fore-gut, the two dorsal aortæ establish their communications with the "primary" heart rudiment even before the latter is completely separated into two endothelial tubes.

The next phase of development of the heart is the appearance of the two separate endothelial tubes, one on each side of the median plane. Each tube is continuous cranially with the dorsal aorta and caudally with the vitelline vein. As development proceeds they tend to grow towards the median plane, and in this way the part of the splanchnic wall of the pleuro-pericardial cavity which lies between them is pushed ventrally. The two tubes remain in contact, but not fused, with each other for a time. Owing to the fact that the endothelial tubes grow more rapidly than the pleuro-pericardial cavity, the former are thrown into loops which are separated by constrictions. These dilatations and constrictions indicate in caudo-cranial succession the future sinus venosus, the sino-atrial canal, the atrium, the atrio-ventricular canal, the ventricle, and bulbus cordis. The most dependent and approximating parts of the endothelial tubes are the ventricular portions. They incline more to the right side of the embryo, and are the first to become fused and to form the "secondary" single heart tube.

The myocardium assumes the familiar S-shaped appearance at a stage when the heart is still in the condition of two separate endothelial tubes. The segments and sulci, appearing on the surface of the myocardial tube, do not correspond, in any way, with the dilatations and constrictions of the two underlying endothelial tubes.

ACKNOWLEDGMENTS.

I take this opportunity to express my thanks to Professor Arthur Robinson for the use of the ferret embryos from his collection which he

placed at my disposal. To him I am also grateful for helpful advice frequently asked and readily given.

For the two early human embryos I am grateful to Dr R. W. Johnstone of the Midwifery Department, Edinburgh University, who, as stated, has kindly permitted me to make use of the serial sections.

To the Carnegie Trust my sincere thanks are due for pecuniary support which has greatly facilitated the completion of this part of my research, and a grant to defray the cost of illustrations. The earlier part of the expenses incurred whilst working at the reconstructions has been borne by a grant from the Earl of Moray's Fund, for which I desire to put on record my gratitude.

The illustrations taken from sections of embryos and from drawings have all been photographed by Mr W. Watson of the Royal College of Physicians Laboratory, Edinburgh, under my personal supervision.

Last, but not the least, I am indebted to Mr J. T. Murray for the drawings of figs. 18, 21, 22, 25, 27, and 30, which represent the original reconstructions.

BIBLIOGRAPHY.

1912. Bailey, F. R., *Text-book of Embryology*, 2nd ed., Bailey and Miller, pp. 222–224.

1881. Balfour, F. M., *Comparative Embryology*, vol. ii. p. 524.

1842. Bischoff, *Entwicklungsgeschichte des Kaninchens*, Braunschweig.

1852. Bischoff, *Entwicklungsgeschichte des Meerschweinchens.*

1891. Bonnet, R., *Grundriss der Entwicklungsgeschichte*, Berlin.

1901. Bonnet, R., "Beiträge zur Embryologie des Hundes," Erste Fortsetzung, *Anat. Hefte*, H. 51, Bd. xvi.

1907. Bonnet, R., *Lehrbuch der Entwicklungsgeschichte*, Berlin.

1889. Born, G., "Heart, Rabbit," *Archiv für mikroscopische Anatomie*, Bd. xxxiii. pp. 284–378.

1905. Bremer, J. L., "Description of a 4 mm. Human Embryo," *Amer. Jour. of Anat.*, vol. v., No. 4, pp. 459–480.

1912. Bremer, J. L., "The Development of the Aorta and Aortic Arches in Rabbits," *Jour. of Anat.*, vol. xiii. pp. 111–128.

1914. Bremer, J. L., "The Earliest Blood-vessels in Man," *Amer. Jour of Anat.*, vol. xvi., No. 4, p. 464.

1908. Bryce, T. H., *Quain's Anat.*, vol. i., "Embryology," p. 62.

1882. Bütschli, O., "Ueber eine Hypothese bezuglich der phylogenetischen Herleitung des Blutgefassapparates eines Theil der Metazoon," *Morphol. Jahrbuch*, Bd. viii.

1910. Dandy, W. E., *Amer. Jour. of Anat.*, vol. x.

1912. Debeyre, A., *Journal de l'Anat. et de la Physiol.*, vol. xlviii. p. 448.

1895. Eternod, A. C. F., "Communication sur un œuf humain avec embryon excessivement jeune," *Arch. Ital. de Biologie*, xxii.: XIe Congrès International des Science Médicales, pp. xii–xiv.

1899. Eternod, A. C. F., "Il y a un canal notochordal dans l'embryon humain," *Anatomische Anzeiger*, xvi. pp. 131–143.

1909. Evans, H. M., "On the Development of the Aorta, Cardinal and Umbilical Veins, and the other Blood-vessels of Vertebrate Embryos from Capillaries," *Anat. Record*, vol. iii. pp. 498–518.

1912. Evans, H. M., "Description of the Vascular System present in Early Human Embryos," Keibel and Mall, *Manual of Human Embryology*, vol. ii. pp. 571, 588, 595.

1897. Felix, W., "Beiträge zur Entwicklungsgeschichte der Salmoniden," *Anat. Hefte*, Bd. viii.

1910. Felix, W., "Zur Entwicklungsgeschichte der Rumpfarterien des menschlichen Embryo," *Morph. Jahrb.*, Bd. xli., Heft 4, S. 577.

1910. Fetzer, "Ueber ein durch Operation gewonnenes menschliches Ei, das in seiner Entwicklung etwa dem Peterschen Ei entspricht," *Ver. Anat. Ges.*, Erg. Heft des *Anat. Anz.*, Bd. xxxvii. S. 116–126.

1907. Frassi, L., "Ueber ein junges menschliches Ei *in situ*," *Arch. für mikr. Anat.*, Bd. lxx. S. 482.

1908. Frassi, L., "Weitere Ergebnisse des Studiums eines jungen menschlichen Eies *in situ*," *Arch. für mikr. Anat.*, Bd. lxxi. S. 667–694.

1912. Gräper, L., "Beobachtung von Wachstumsvorgängen an Reihenaufnahmen lebender Hühnerembryonen nebst Bemerkungen über vitale Färbung," *Archiv für Entwicklungsmechanik der Organismen*, Bd. xxxiii.

1895. Grosser, O., and Brezina, E., "Ueber die Entwicklung der Venen des Kopfes und des Halses bei Reptilien," *Morph. Jahrb.*, Bd. xxxiii.

1913. Grosser, O., and Brezina, E., "Ein menschlichler Embryo mit Chordal Kanal," *Anat. Hefte*, Bd. xlvii. S. 653–686

1909. Hahn, H., "Experimentelle Studien ueber die Entstehung des Blutes und der ersten Gefässe beim Hühnchen," *Arch. für Entwicklungsmechanik der Organismen*, Bd. xxvii.

1876. Hensen, V. von, "Beobachtungen ueber die Befruchtung und Entwicklung des Kaninchens und Meerschweinchens," *Zeitschr. für Anat. u. Entwicklungsgeschichte*, Bd. i.

1892. Hertwig, O., "*Text-book of the Embryology of Man and Mammals*, pp. 176–186, 542–548.

1909. Herzog, M., *Amer. Jour. Anat.*, vol. ix. p. 361.

1875. His, W., "Der Keimwall des Hühnereies und die Entstehung der parablastischen Zeller," *Zeitschr. f. Anat. u. Entwicklungsgeschichte.*

1881. His, W., "Mitteilungen zur Embryologie der Säugetiere und des Menschen," *Archiv f. Anat. u. Phys.*

1885. His, W., *Anatomie menschlichler Embyronen*, III. i., Leipzig.

1886. His, W., *Beiträge zur Anatomie des menschlichen Herzens*, Leipzig.

1900. His, W., "Lecithoblast und Angioblast der Wirbeltiere," *Abh. d. math.-phy. Klasse d. Kgl. Säch. Ges. d. Wiss.*, Bd. xvi., Leipzig.

1910. Huntington, G. S., "The Phylogenetic Relations of the Lymphatic and Blood Vascular System in Vertebrates, and the Genetic Principles of the Development of the Systemic Lymphatic Vessels in the Mammalian Embryo," *Anat. Rec.*, vol. iv. p. 339.

1914. Huntington, G. S., "The Development of the Mammalian Jugular Lymph-sac, of the Tributary Primitive Ulnar Lymphatic, and of the Thoracic Ducts from the view-point of recent investigations of Vertebrate Lymphatic Ontogeny; together with a consideration of the Genetic Relations of Lymphatic and Hæmal Vascular Channels in the Embryos of Amniotes," *Amer. Jour. Anat.*, vol. xvi.

1914. Johnstone, R. W., "Contribution to the Study of the Early Human Ovum, based upon the investigation of (I.) a very early Ovum embedded in the Uterus, and (II.) a very early Ovum embedded in the Infundibulum of the Tube," *Jour. of Obstetrics and Gynæcology of the British Empire*, May, pp. 231–276.

1907. Jung, *München med. Wochenschr.*, Jahrg. liv. p. 1343.

1888. Keibel, F., "Die Entwicklungsvorgänge am hinteren Ende des Meerschweinchenembryos," *Arch. f. Anat. u. Phys.*

1908. Keibel u. Elze, *Normentafel zur Entwicklungsgeschichte des Menschen*, Jena.

1861. Kölliker, A., *Entwicklungsgeschichte des Menschen und der hoheren Thiere*, Leipzig.

1882. Kölliker, A., *Die Entwicklung der Keimblätter des Kaninchens:* Festschrift, Leipzig.

1884. Kölliker, A., "Die embryonalen Keimblätter und die Gewefe," *Zeitschr. für wiss. Zoologie*, Bd. xxxiv.

1904. Lewis, F. T., "The Intra-embryonic Blood-vessels of Rabbits from 8½–13 days," *Amer. Jour. of Anat.*, vol. iii., No. 1, pp. 12–13.

1908. Low, Alex., "Description of a Human Embryo of 13–14 Mesodermic Somites," *Jour. of Anat. and Phys.*, vol. xlii. (ser. iii., vol. iii., part iii.), pp. 237–251.

1912. Mall, F. P, "On the Development of the Heart," *Amer. Jour. of Anat.*, vol. xiii. pp. 249–298.

1912. Mall, F. P., "A Human Embryo 26 days old," *Jour. of Morph.*, vol. v. pp. 459–480.

1909. Maximow, A., "Die Frühesten Entwicklungsstadien der Blut- und Bindegewebzellen beim Säugetierembryo, bis zum Anfang der Blutbildung in der Leber," *Archiv für mikr. Anat.*, Bd. lxxiii.

1910. M'Clure, C. F. W., "The Intra-intimal Theory and the Development of the Mesenteric Lymphatics in the Domestic Cat (*Felis domestica*)," *Verhandl. der Anat. Gesellsch.*

1912. M'Clure, C. F. W., "A few Remarks relative to Mr Kampmeier's Paper on the Value of the Injection Method in the Study of Lymphatic Development," *Anat. Rec.*, vol. vi.

1914. Miller, A. M., and M'Whorter, J. E., "Experiments on the Development of Blood-vessels in the Area Pellucida and Embryonic Body of the Chick," *Anat. Rec.*, vol. viii.

1912. Minot, C. S., "The Origin of the Angioblast and the Development of the Blood," Keibel and Mall, *Manual of Human Embryology*, vol. ii. p. 499.

1906. Mollier, S., "Die Entwicklung der Gefässe im Embryo," *Handb. vergl. u. expt. Entwickl. d. Wirbeltiere*, herausg. von O. Hertwig, Bd. i., Kap. v., S. 1261.

1915. Parker, Katharine, M., "The Early Development of the Heart and Anterior Vessels in Marsupials, with special reference to Perameles," *Proceedings of the Zoological Society of London*, pp. 459–499.

1886. Rabl, C., "Ueber die Bildung des Herzens bei Amphibien," *Morph. Jahrb.*, Bd. xii.

1915. Reagan, "Vascularisation Phenomena in Fragments of Embryonic Bodies completely isolated from Yolk-sac Blastoderm," *Anat. Rec.*, vol. ix., No. 4.

1892. Robinson, A., "Observations upon the Development of the Segmentation Cavity, etc.," *Quart. Jour. of Miscrocs. Science*, N.S., vol. xxxiii.

1902. Robinson, A., "The Early Stages of the Development of the Pericardium," *Jour. of Anat. and Phys.*, vol. xxxvii. p. 15.

1916. Robinson, A., and Gibson, A., "Description of a Reconstruction Model of a Horse Embryo Twenty-one Days Old," *Transactions of the Royal Society of Edinburgh*, vol. li., part ii. (No. 8), p. 340.

1904. Rouvière, H., "Etudes sur le développement du péricarde chez le lapin," *Jour. de l'Anat. et de la Phys.*, xl.

1906. Rückert u. Mollier, "Die Entstehung der Gefässe und des Blutes bei Wirbeltieren," *Handb. vergl. u. expt. Entwickl. d. Wirbeltiere*, herausg. von O. Hertwig, Bd. i. S. 1019.

1892. Schmidt, M. B., "Ueber Blutzellenbildung in Leber und Milz, etc.," *Zeigler's Beiträge*, Bd. xi.

1915. Schulte, H. von W., "The Fusion of the Bilateral Anlagen of the Heart and the Formation of the Bulbo-ventricular Loop in Embryos of the Cat," *Proceedings of the Amer. Assn. of Anatomists*, p. 72.

1889. Shore, T. W., "The Proamnion and Amnion in the Chick," *Jour. of Anat. and Phys.*, vol. xxiv. p. 6.

1902. Sobotta, J., "Ueber die Entwicklung des Blutes, des Herzen und der grossen Gefässstämme der Salmoniden nebst Mitteilungen ueber die Austildung der Herzform," *Anat. Hefte*, 63 (Bd. xix., Heft 3).

1889. Spee, Graf, "Beobachtungen an einer menschlichen Keimscheibe mit offener medullarrinne und canalis neurentericus," *Arch. f. Anat. u. Phys., Anat. Abt.*, S. 159.

1896. Spee, Graf, "Neue Beobachtungen ueber sehr frühe Entwicklungsstufen des menschlichen Eies," *Arch. f. Anat. u. Phys., Anat. Abt.*

1915. Stockard, Charles R., "The Origin of Blood and Vascular Endothelium in Embryos without a Circulation of the Blood and in the Normal Embryo," *Amer. Jour. of Anat.*, vol. xviii., No. 2.

1915. Stockard, Charles R., "A Study of Wandering Mesenchymal Cells on the Living Yolk-sac, and their Developmental Processes: Chromatophores, Vascular Endothelium, and Blood-cells," *Amer. Jour. of Anat.*, vol. xviii., No. 3, pp. 525–594.

1883. Strahl, H., "Ueber die Anlage des Gefässsystems in der Keimscheibe von *Lacerta agilus*," *Marb. Sitzungsber.*

1899. Stricht, C. van der, "L'origine des premières cellules sanguines et des premiers vaisseaux sanguins dans l'aire vasculaire de chauves-sauris," *Bull. de l'Acad. Roy. de méd. de Belgique*, t. xiii. p. 4.

1912. Tandler, J., "The Development of the Heart," Keibel and Mall, *Manual of Human Embryology*, vol. ii. p. 534.

1884. Türstig, J., "Untersuchungen ueber die Entwicklung der primitiven Aorten," *Schrift herausgegeben v. d. Naturf.-Ges. bei d. Univ. Dorpat*, Bd. i., Dorpat.

1892. Vialleton, L., "Développement des aortes chez l'embryon de poulet," *Jour. de l'Anat. et de la Phys.*, t. xxviii. p. 1.

1913. Wallin, Ivan E., "A Human Embryo of 13 Somites," *Amer. Jour of Anat.*, vol. xv., No. 3, pp. 319–332.

1915. Watt, J. Crawford, "Description of Two Young Twin Human Embryos with 17–19 Paired Somites: Contribution to Embryology, No. 2," *Carnegie Institution of Washington Publication*, No. 222, pp. 5–44.

1910. Weidenreich, F., "Die Morphologie der Blutzellen und ihre Beziehungen zu Einander," *Anat. Rec.*, vol. iv. p. 317.

1914. Wilson, J. T., "Observations upon Young Human Embryos," *Jour. of Anat. and Phys.*, vol. xlviii. (series iii., vol. ix., part iii.), pp. 315–351.

1911. Yeates, Thos., "Studies in the Embryology of the Ferret," *Jour. of Anat. and Phys.*, vol. xliv. (ser. iii., vol. vi.), pp. 319–335.

1915. Yeates, Thos., "Studies in the Embryology of the Ferret," *Studies in Anatomy*, Birmingham University, pp. 71–107.

1887. Ziegler, H. E., "Die Entstehung des Blutes bei Knochenfischembryonen," *Arch. f. mikr. Anat.*, Bd. xxx.

1892. Ziegler, H. E., und Ziegler, E., "Beiträge zur Entwicklungsgeschichte von Torpedo," *Arch. f. mikr. Anat.*, Bd. xxxix.

THE REPRODUCTIVE ORGANS OF CETACEA.

By Professor Alexander Meek, *Armstrong College, Newcastle-on-Tyne.*

The Cetacea have become modified for aquatic life, and it has been an interesting task for the morphologist to trace the changes which have been brought about by a more and more complete adaptation to the habitat. The reproductive organs are peculiarly interesting in this respect, for all the events connected with reproduction take place in aquatic and pelagic conditions.

The general disposition of the organs and their general morphology are already known from the investigations made by Weber, Guerin, Rapp, Van Beneden, Hunter, Owen, Cleland, and recently by Hepburn; but the modifications they present in relation to function do not appear to have been clearly stated, and I find it necessary, therefore, to give a re-statement of the facts of structure with reference to some of the common Delphinidæ.

About 1889–1890 I had the opportunity of examining male fœtuses of various toothed whales in the laboratory of Professor D'Arcy W. Thompson, Dundee, and it was the intention to publish the results in the series of researches which were at that period issued from his department. But financial difficulties intervened and the series came to an end. I have the permission of Professor Thompson to incorporate in this paper the figures which were made so long ago.

This year, 1917, the fishermen at Cullercoats have captured many porpoises in the salmon drift-nets, and the investigation of some of these gave the opportunity of re-examining the structural modifications. Although this species is the one which has been most frequently examined, it will be convenient to describe as fully as is necessary the organs in both sexes.

The sexes are easily distinguished. In the female the anal and vulval openings are close together, and may indeed occupy the same recess. On each side of the vulva is the slit-like opening in which is lodged the teat of the mammary gland. In the male the similar opening of the preputial pouch is centrally situated, and the anal opening is far removed from it posteriorly. In front of the latter is a small aperture in which the reduced teats of the mammary gland are situated.

Phocæna communis. Female. (Figs. 1 and 2.)

The females examined, four in number, measured 4 ft. 3 ins. to 4 ft. 5 ins. in length, and the anterior end of the vulval opening was situated about 2 ft. 5 ins. to 2 ft. 7 ins. from the anterior end. The vulva varied from 3 to 4½ ins. in length. The anal opening is usually separated from the vulval opening by a ridge, but, as has already been stated above, it may actually be enclosed in the vulval aperture.

In all respects, except at the uterine end of the vagina, the organs have a simple structure. The elongated, only slightly wrinkled ovaries are situated on the dorsal proximal aspect of the Fallopian tube. The Fallopian tube is much coiled, and ends in a uterus which, meeting its fellow, descends without fusion to open just above the os in a small part of the uterus common to both tubes. The cervix descends into the vagina as a short cylindrical structure. It is beset externally with numerous deep, longitudinal folds which are continued into the canal leading from its free flattened vaginal surface to the uterus.

The vagina is much modified in the region next to the uterus; the ventral wall is continuous with, or occupies practically the same plane as, the uterus, but the dorsal wall is distended into a cavity which forms a prominent swelling. Associated with this expansion are certain folds of the vaginal walls, which clearly subserve an important function. The transverse folds of the mucous membrane of the upper part of the vagina are highly developed, and in addition two immense folds, almost encircling the vagina, convert the upper part of the tube into a recess which may be called the spermathecal recess (fig. 1). The upper fold springs from the ventral wall, thus serving to occlude the cervix and the os. The other is a similar transverse outgrowth of the dorsal wall, which carries the opening from the vagina into the spermathecal recess to the ventral side. The folds which define this chamber are clearly liable to be moved backwards and forwards, but it is important to note that in their normal disposition they form a passage from the vagina proper to the spermathecal recess of the vagina, which begins as a narrow opening on the ventral side and is continued between the two folds as a passage which opens into the recess dorsally.

Immediately below the folds the vagina is a spacious cavity, wrinkled internally by transverse and longitudinal shallow grooves, and it has a smooth and velvety surface. The transverse grooves are more prominent in the upper region of the vagina, and the longitudinal in the lower, a few of these latter extending into the vulva. The aperture between the vagina and vulva is a very small one. The sphincter vaginæ muscle is well

developed, encircling the tube in this region, and under usual conditions practically closes the passage.

The external opening extends from the anus, or immediately in front of the anus, forwards as a long slit leading into a flattened, roomy cavity, rapidly narrowing to the opening into the vagina. The lateral walls are more or less grooved, and the anterior angle is occupied by the clitoris. The latter forms a prominent ridge, and ends near the vaginal opening in a distinct glans-like projection. Anteriorly it divides into two arms or crura, which, however, have nothing to do with the corpora cavernosa. Each corpus arises from the pelvic bone in the same region as that of the male, and, descending on the internal side of the erector muscle, the two fuse as

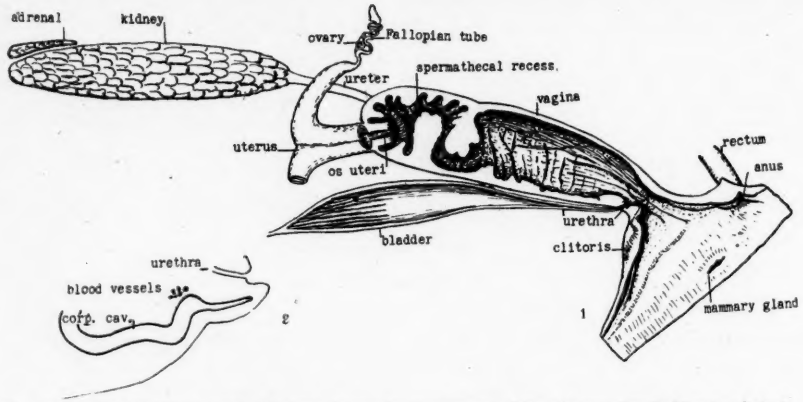


FIG. 1.—1, Longitudinal sectional view of reproductive organs of female porpoise (half natural size); 2, sectional drawing of clitoris to show disposition of corpus cavernosum (natural size).

the muscles do above the clitoris. The single corpus cavernosum, resulting from the fusion, enters the clitoris near the middle of the body of that organ and is bent backwards towards the glans. It presents another distinct curve in front of the glans, which it enters, after narrowing considerably, and occupies its ventral free region. The corpus in the clitoris is surrounded by a thin sheath and by erectile and fibrous tissues. The disposition of these structures will be found to be important when the structure of the penis is considered. The glans, it will be noted, is not a true glans, as it is traversed by the corpus cavernosum; but its position and appearance serve to indicate that it is the glans invaded and reinforced by the corpus cavernosum. The clitoris is surrounded by a preputial fold which, beginning above the glans in the urethral prominence, extends on each side to the anterior end of the clitoris, where the two folds approxi-

mate but do not fuse. The folds are especially prominent anteriorly. The disposition of the preputial fold is interesting, since it homologises the external part of the clitoris with the free part of the penis which occupies the preputial pouch of the male. Immediately beyond the clitoris is the opening of the urethra, defined as a medium, short, longitudinal opening between two transverse grooves. It occupies the anterior part of a median prominence just internal to the glans clitoris, and which marks also the beginning of the preputial fold.

As has already been remarked, on each side of the external opening there is a slit which lodges the cylindrical teat of the mammary glands, on the free end of which there is one opening.

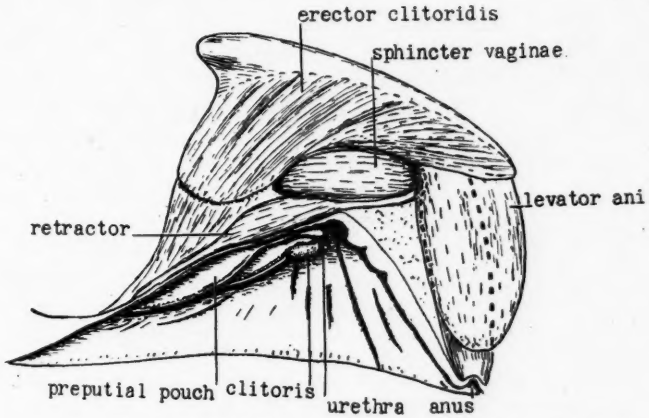


FIG. 2.—Pelvic and associated muscles of female porpoise. (Natural size.)

The muscles of this region are interesting (fig. 2). The pelvic bone is smaller in the female than in the male, but associated with it are the usual muscles and others connected with the external opening. The erector clitoridis springs practically from the whole outward border of the bone. The two muscles practically surround the corpora cavernosa at their origin, the mesial side next the vagina only being uncovered, and the muscles fuse as the corpora do, just above the clitoris, both muscles thus being concentrated in the sheath of the corpus and the neighbouring region of the clitoris. The levator ani arises from the internal border of the pelvic bone and is inserted into the lateral walls of the lower part of the rectum. The sphincter vaginæ is well developed. It encircles, and is connected to, the lower part of the vagina, and it also embraces the urethra. The lower half only is seen in fig. 2, the upper half being covered by the

erector muscle. Below it comes into close association with the clitoris. The retractor clitoridis arises from the rectum, and is associated at its origin likewise with the sphincter; and passing forwards in a tunnel between the erector, the levator ani, and the sphincter, as a long tendon, it expands into a muscle above the clitoris and is inserted at the base of the preputial pouch.

The female organs are thus, apart from the spermathecal folds of the upper part of the vagina, simple and typical. As will be seen, their condition, and especially the presence of the spermathecal recess, helps us to understand the remarkable modifications in the male. The narrow entrance to the vagina may be said to be an adaptation to occluding the cavity of the vagina from the sea, and the spermathecal recess to preventing the semen leaving the vagina on the withdrawal of the penis. The spermathecal recess is a remarkable modification, since it has taken place in spite of the equal periodical difficulties connected with the birth of the young. The deep folds of the upper part of the vagina permit of considerable distension, and are evidently modifications connected with birth.

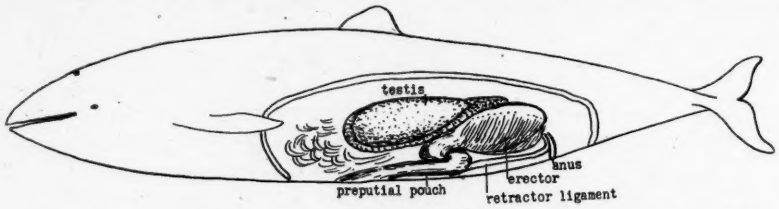


Fig. 3.—Diagram to show disposition and relative size of mature male organs of porpoise measuring 4 ft. 5 ins.

Phocæna communis. Male. (Figs. 3–7.)

In the male the testes undergo an enormous development in the summer, as will be apparent from fig. 3, which indicates the relative disposition of the organs in a mature male measuring 4 ft. 5 ins. They also increase greatly in weight; one testis in this male weighed 500 grams, in another 600 grams, and in still another 700 grams. On the other hand, in a male measuring 4 ft. the testis was only $2\frac{1}{2}$ ins. long and the weight 1–2 grams. Associated with the huge testis the epididymis is highly developed. The duct becomes much folded posteriorly to the testis, and the folds are still retained as the vas deferens passes to the space between the bladder and the ureter. The two vasa deferentia approach one another behind the bladder and pass downwards side by side to open separately

on the eminence of the floor of the urethra, called the verumontanum. Between the openings, and slightly posterior to them, the verumontanum presents another, or a pair of openings which lead into a blind tube lying between and behind the terminal ends of the vasa deferentia. The opening is crescent-shaped, and may be single or paired, but in each case the cavity is a single one occupied by a slight ridge projecting from the floor. From its position this tube, with its single or double opening, answers to the uterus masculinus or sinus pocularis. In the porpoise the sinus has usually two apertures on the verumontanum. The vasa deferentia and the epididymes are highly developed and are capable of containing a large quantity of sperms. It is to be noted that seminal vesicles are absent.

In this region of the urethra the numerous ducts of the prostate glands open along parallel lines in the depression on each side of the verumontanum, below the level of the openings of the vasa deferentia. They thus lie near the angle where the first sharp bend of the urethra takes place. The verumontanum begins at the base of the bladder as a narrow ridge expanding to receive the ducts above mentioned opposite the prostate glands, and it narrows again in the region occupied by the ducts of the prostate gland. Cowper's glands are absent.

The urogenital duct beyond the prostatic region is surrounded by penial structures, the disposition of which is highly interesting. The duct itself is enclosed by a corpus spongiosum, which, beginning in a bulb, extends to the tip of the penis. The corpora cavernosa arise from the pelvic bones, and in passing between those bones unite almost immediately to form a single corpus cavernosum, which extends likewise to nearly the end of the penis. The corpus cavernosum consists of a vascular part surrounded by a tough fibrous sheath, and the disposition of each of these in the various regions will be plain from an inspection of fig. 6. The sheath expands postero-medially near its origin into a process, rectangular in section. The process invades the accelerator muscle; the two processes approach one another below the prostate gland and almost meet behind it. In this region the processes are connected by a thin fascia. It will be seen from fig. 4 that at the anterior end the corpus cavernosum is suddenly reduced to a rounded shape together with its sheath, and is thrown into a distinct fold, being bent downwards and to the right side before running forwards to the end of the penis; the meaning of this will be discussed presently. The anterior end of the penis is enclosed in a preputial pouch, the skin of which, both that of the pouch and that covering the penis, is remarkably thin. That of the pouch is thrown into longitudinal folds allowing of lateral distension. The opening is like that of the vulva, but it is situated practically in the middle of the body, and the pouch is also con-

stricted to a narrow opening at about the same depth as that of the vulva. The free part of the penis occupying the pouch is, because of the bend in the corpus cavernosum mentioned above, sharply resolved into two regions—a proximal, continuous with and having the same structure as the main body of the penis, and a distal, which is long, narrow, and almost round in section. The urethra opens by a longitudinal slit on the ventral aspect of this latter part of the penis near the tip (figs. 4 and 6).

The whole structure, from the prostatic part of the urethra to the free part of the penis in the resting condition, is thrown into (1) the fold mentioned above at the origin; (2) the double fold shown in fig. 3, involving

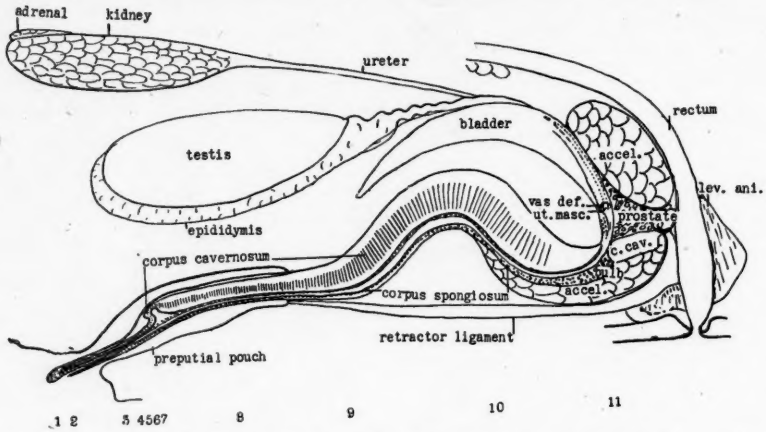


FIG. 4.—Longitudinal sectional view of reproductive organs of male porpoise. (Half natural size.) *c cav.*, on the right, points to the tendon-like process of the sheath of the corpus cavernosum which invades the accelerator muscle.

nearly the whole of the proximal part of the penis behind the preputial pouch. The corpus cavernosum of the clitoris presents similar folds; compare figs. 1 and 4.

The penis is highly developed, and the muscles associated with it are strong and massive. The erector penis muscle arises from the whole length of the large pelvic bone, and is inserted into the sheath of the corpus cavernosum as far forwards as near to the beginning of the second fold mentioned above. The two muscles enclose the corpora cavernosa at their origin, and each corpus is also attached to the pelvic bones by a strong ligament extending to near the anterior extremity of the bone. The accelerator urinæ muscle is especially strongly developed around the bulb and the prostate; the fibres are concentrated in the process of the sheath

of the corpus cavernosum mentioned above. The processes and the fascia connecting them serve to separate the prostate gland above from the bulb

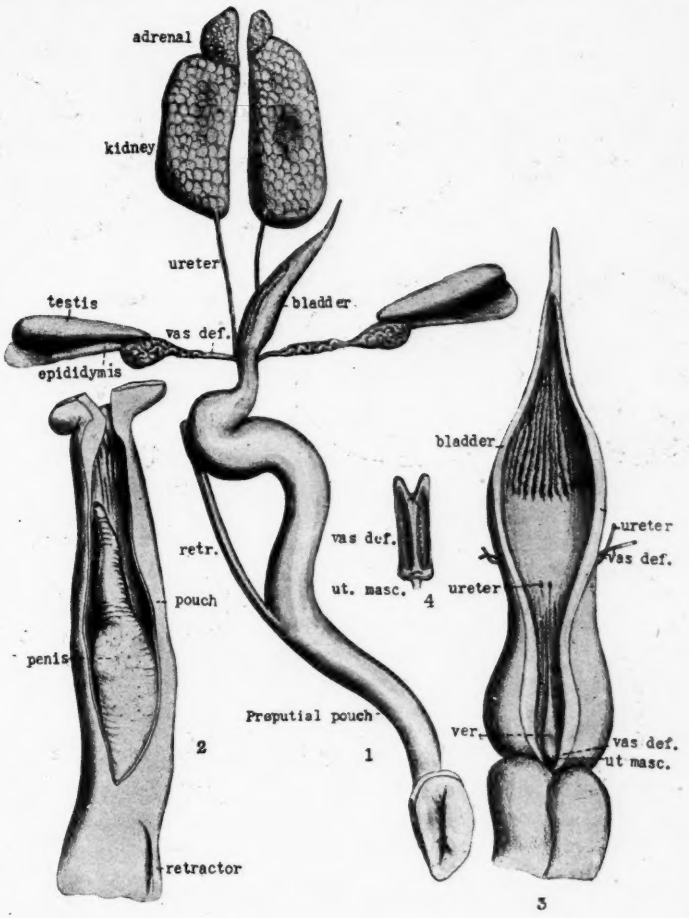


FIG. 5.—General dissection of the reproductive organs of male porpoise. 1, The general relationship of the organs in the adult, but immature, state; 2, the preputial pouch and penis; 3, the bladder and verumontanum region of the urethra; 4, dissection of verumontanum.

below. A strong, double, elastic retractor ligament extends from the rectum, and the transverse process of the sheath of the corpus cavernosum, forwards

below the accelerator muscle to be inserted into the base of the preputial pouch.

This is the general structure with reference to the penis in the retracted

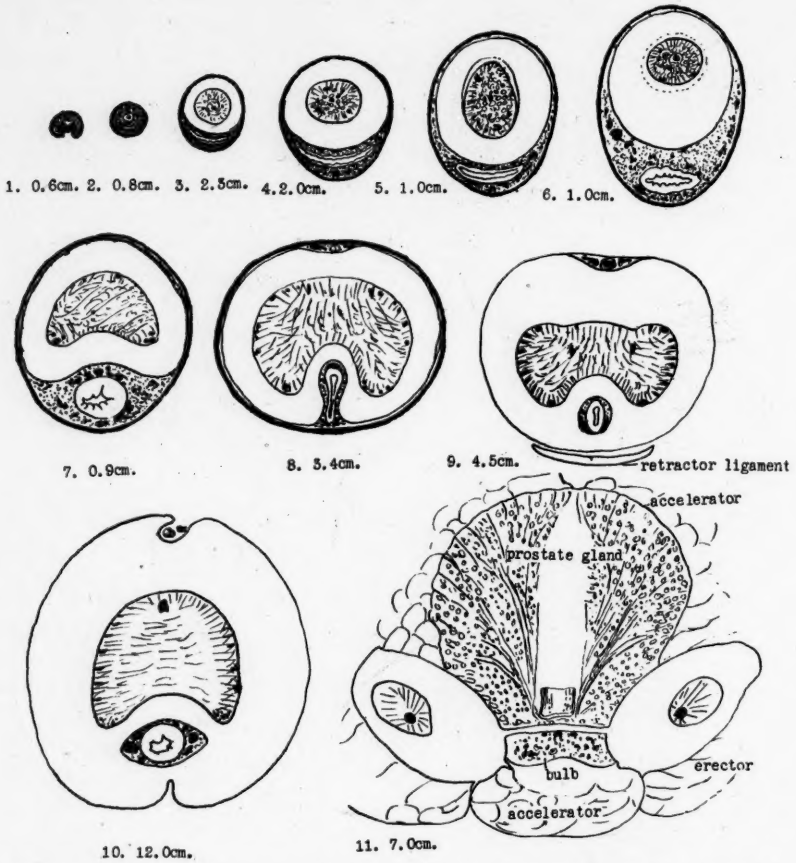


FIG. 6.—Transverse sections of penis of porpoise. The numbers below fig. 4 indicate the levels of the successive sections. The sheath of the corpus cavernosum is unshaded.

condition, when it is withdrawn within the preputial pouch. In a state of erection the penis may be protruded to a length which brings the tip as far forwards as opposite the pectoral fin, even the pectoral girdle. As will be seen from fig. 3, its direction during erection is forwards and only at a

small angle outwards; and as will be seen further from fig. 7, the erection brings about a remarkable change in the disposition of the proximal and distal parts of the preputial portion of the penis. They become still more sharply defined, the proximal part being stiff and hard, like the main part of the penis posteriorly, while the distal, terminal part remains pliable, especially where the two parts are joined together. In attaining this condition a corkscrew-like movement is given to this terminal part of the penis.

It has already been noted that the vagina is relatively short. In the female figured it measured, from the opening of the vagina to the second fold, 7·5 cm., and in another female about 9 cm. The latter is just about the length of the distal end of the erected penis. It is evident, therefore, that this is the only part of the penis which enters the vagina.

The pairing of these creatures must be a difficult proceeding, and the

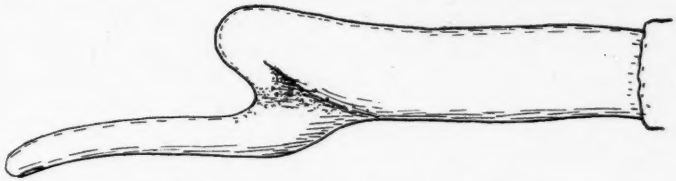


Fig. 7.—The preputial part of the penis when erected.

above structural modifications are meant to make it effective. They apparently range themselves in ventral apposition in such a manner as to bring the respective openings together. The head of the female will therefore be in advance of that of the male. The latter may be able to assist matters with his pectoral fins, and the female by flexing the caudal fin so as to form a groove for the body of the male. When erection takes place, the first part of the penis to emerge is the narrow, free end, which will therefore enter the vulva, and the rotation which is being communicated to it will enable it to gain access to the vagina; the blunt end of the proximal part of the penis will abut against the front wall of the vulva, adapting itself to the clitoris. The direction of the free end of the penis is such that it will pass the first fold of the vagina and bend upwards the second. The outlet of the penis is on the ventral side near the tip, and consequently the discharge is projected into the spermathecal recess. The bulb is compressed as well as the prostate by the accelerator muscle, and it is evident, therefore, that the terminal part of the penis is subject to a slight expansion during ejaculation. It is evident, also, that as a result of the erection the female is carried forwards and some little distance away

from the male, and at this period the bodies of the two may be subject to some degree of rotation. This is met by the joint in the penis at the base of the copulatory part, allowing for a wide range of movement. From this it may be gathered that discharge follows immediately, for any movement will likely result in separation. When the discharge has taken place and erection ceased, the retractor ligament withdraws the penis once more into the preputial pouch. In all the males examined a discharge, rich in spermatozoa, could be obtained by simply pressing the penis, and sometimes even without. Living sperms were obtained in this way a day after death. The immature males similarly yielded a discharge, but the ejaculate did not contain sperms. In both cases the ejaculate contained other cells, as prismatic cells from the vasa deferentia and lymphocytes. The immature males are apparently capable of conjugation, for they have been captured in the same part of the net as the females.

The fact that the urogenital duct is filled with the spermatic fluid in the mature male, and with a discharge in the immature male, points to a recent copulation. But this simple and obvious conclusion does not meet the conditions. A male was brought in injured but alive, and remained in the floor pool for a couple of days before it died. In this case also the urogenital duct was fully occupied by sperms. It cannot be said, then, that copulation had taken place sufficiently recently to account for this, for urination must have occurred in the meantime, and that this was so was indicated by the small quantity of urine in the bladder.

We may take it that in the act of micturition the bladder is emptied, and it is the function of the accelerator urinæ muscle to clear the urine from the urogenital duct of the penis. The difference between this act and that of discharge during copulation is that the pulsations of the accelerator eject the contents of the urogenital duct, which is filled immediately by the simultaneous peristaltic contractions of the vasa deferentia. In the case of urination there is no supply to draw upon; in the other there is a supply. We can thus account for the penial part of the duct being filled with sperms after copulation, but it is evident that the duct will be cleared of sperms at the next urination.

We can only account, then, for the presence of sperms in the urogenital duct in the above cases by a choice between two explanations. The first is that the pressure of sperms into the duct is steadily maintained by the contraction of the vasa deferentia apart from copulation; the second is that erection and discharge has taken place as a result of drowning.

The first explanation is not satisfactory, for in the resting condition the penis is not at all likely to be thus so completely occupied by the spermatic fluid injected. It is not likely, either, that the duct will be in this

way filled and emptied at every act of urination. It is also necessary to take note of the fact that in no case had the females associated with the males been in copulation, for the vagina and the spermathecal recess were free of sperms. Yet in the case of two of the females a discharge was freely issuing from the narrow opening of the vagina, bathing the clitoris. In all the females the spermathecal recess was occupied by a thick, viscid uterine discharge, although the latter may have had no connexion with the immediate act of copulation. The absence of sperms in these added evidence of significant value pointing to the second explanation, and that both sexes are affected.

There cannot be any doubt, however, that pairing takes place in the summer, although, so far, we have not obtained a female which shows that it had actually taken place. This may be due to the female immediately after the event quitting the inshore waters.

The penis, then, is greatly modified in the porpoise, the copulatory part being differentiated from the rest, from which it is separated by a joint allowing of a wide range of movement. In the state of erection it is still pliable, and it may therefore be said to be adapted to obtaining easy access to the vagina, to changes of position of the bodies of both the male and the female, and also to yielding to pressure if access to the vagina has not been obtained.

It is probable, therefore, that the preputial pouch has a vaginal importance, and, in the case of successful copulation, the copulatory part of the penis is, because of the continuity to begin with between the preputial pouch and the vagina, prevented from coming into contact with the water, as the rest of the free part of the penis must do during erection.

The prevalence of porpoises near the shore during the summer months when drift-net fishing is taking place, and their absence at other seasons, have led to the conclusion that their advent is due to their feeding on salmon. In the case of all those that were examined it is interesting to point out that food was only obtained in the stomach of two, a female and an immature male, and in each case it was gadoid, probably young whiting, much digested.

There is no doubt that at this season, July and August, the porpoises are pairing, and their appearance near the shore at this period may be described, therefore, as a migration for that purpose. It is also fairly clear that in the region where the salmon-fishing takes place males are more commonly captured than females. It seems warrantable to conclude that the males frequent the inshore waters and the females enter the region when they come into season, departing after pairing has taken place. Mr W. J. M. Menzies of the Scottish Fishery Board has informed me that

four porpoises caught in the salmon nets on the shores of the Moray Firth and which he examined, were all males. Porpoises are common both in the Atlantic and Pacific, and no doubt in both regions an inshore migration takes place for the birth of the young and for pairing.

Lagenorhynchus albirostris. An abnormal male.

This white-beaked dolphin, which measured 5 ft. 2 ins., was caught in the salmon nets on the north side of the mouth of the Tyne, and was landed at Cullercoats on August 24, 1911. The urogenital organs were removed and preserved by Mr Storrow. They were labelled "male," and they prove on examination to be essentially male, but they are so abnormal in position and structure as to warrant a somewhat detailed description.

In the first place, the preputial pouch, instead of being central in position, is far back, close to the anus, thus in the position of the vulva. The free part of the penis is very short, only $3\frac{1}{2}$ ins. long, but has the gradually tapering shape and the structure of the species. The pouch is proportionally short; its wall is furrowed, but is more like the vagina in structure. It is constricted externally into a narrow neck, and the anterior angle of the external opening is occupied by two ridges which almost suggest a clitoris in appearance. The position of the mammary glands could not be ascertained, as the posterior part of the pouch had been removed, but it is more than probable that they were paired and situated on either side of the preputial pouch. In association with the short pouch and the near proximity of the rectum, the retractor ligament only measured about $1\frac{3}{4}$ in. It was inserted at the base of the preputial pouch. The proximal part of the penis between the preputial pouch and the prostatic region is also strikingly short, although it presents the usual folds of the normal condition. It is flexed ventrally from the region of the prostatic ducts, and is then directed dorsally to the left side and again to the right before it enters the pouch. This is the normal disposition, but the whole structure is dwarfed. The urogenital duct is that of the male, and ends in a horizontal slit terminally; and this is also the normal condition.

A small prostate is present, and the ducts open as usual below the openings of the verumontanum. The expanded portion of the verumontanum presents the paired openings of the vasa deferentia, and below them the Λ-shaped opening of the uterus masculinus.

But what makes the specimen particularly interesting is the presence of small testes, each with an epididymis and a coiled Wolffian duct, together with a Müllerian duct. The Müllerian ducts meet and fuse, but they are altogether unconnected with the uterus masculinus, which latter has the normal disposition (fig. 9). It is difficult to imagine the circumstance which

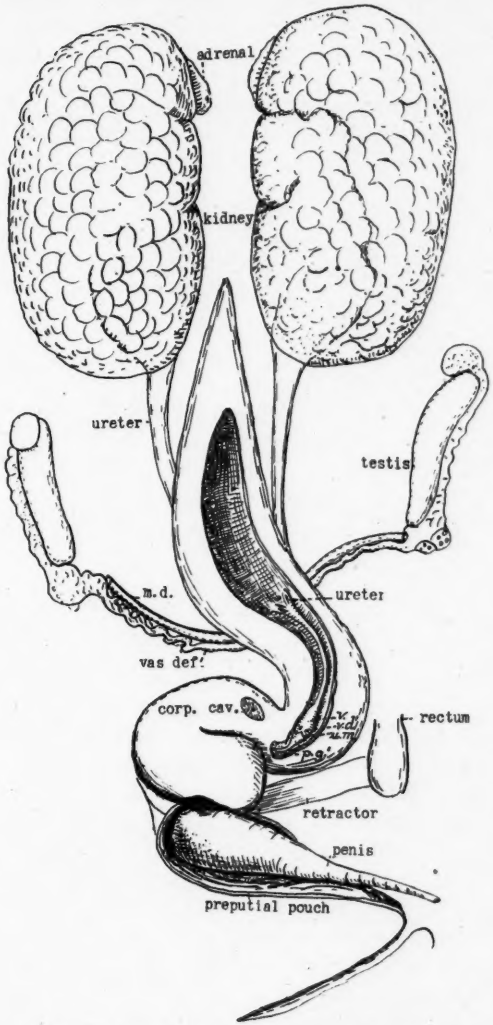


FIG. 8.—The general disposition of the organs of an abnormal male *Lagenorhynchus albirostris*, in ventral view. (Half natural size.)

v., verumontanum; *v.d.*, opening of vas deferens; *u.m.*, uterus masculinus; *p.g.*, opening of prostate gland; *m.d.*, Müllerian duct.

has led to a disappearance of the oviduct in the interval separating the uterus masculinus from the Müllerian duct, and this feature raises, therefore, some degree of doubt as to the identity of the sinus pocularis with the Müllerian duct.

The bladder and the kidneys and ureters are in striking contrast (as will be seen from fig. 8) with the rest of the structures as regards size.

Sections were made of the testis at different levels. They were found

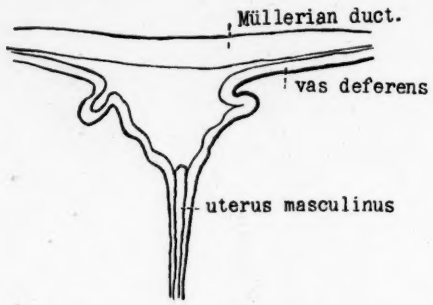


FIG. 9.—The relationship of the Müllerian and Wolffian ducts in the abnormal Lagenorhynchus.

to present numerous tubules of the usual character, but no ova were to be seen.

Lagenorhynchus albirostris. The normal male organs.

Fortunately, I have drawings of the normal male organs of a fœtus of *Lagenorhynchus albirostris*, which are produced here in fig. 10, and which will be described briefly with especial reference to the abnormal specimen an account of the organs of which has just been given. These were made long ago, as has been stated, in the Zoological Department of the University College, Dundee.

The disposition of the organs in the body is already well known,[1] and it is almost exactly the same as in the porpoise. The penis, it will be observed, is situated forwards from the anus, and in front of the latter are the small paired openings of the mammary glands. Internally, the organs except in their general relationship, are very like those which have just been described in the abnormal specimen. The testes are elongated, the epididymes are large, each projecting beyond the testis in a caput epididymis (the latter is somewhat exaggerated in the abnormal specimen). The

[1] Hunter, *Structure and Œconomy of Whales.* Cleland, *Journ. Anat. and Phys.*, vol. xviii. p. 334.

vasa deferentia pass as usual from the epididymes to open separately in the verumontanum. The uterus masculinus has a Λ-shaped aperture immediately below the openings of the vasa deferentia, and the shape of the

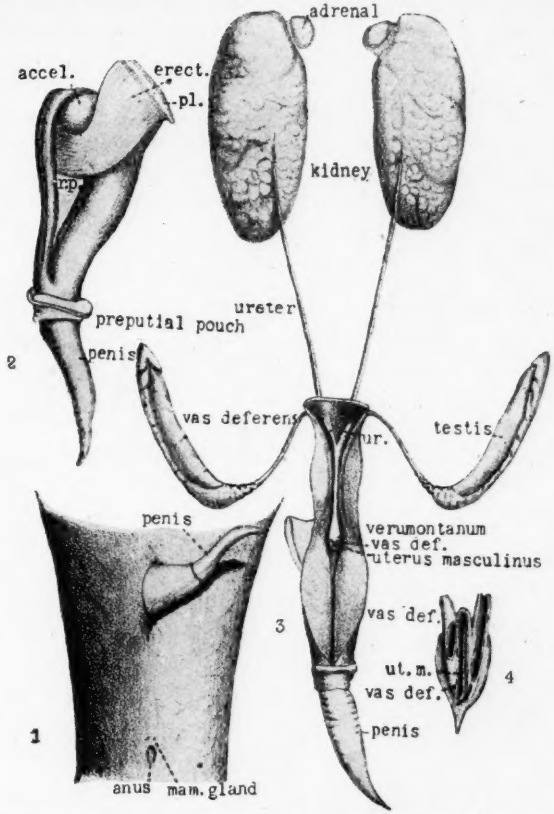


FIG. 10.—The normal male organs of a fœtal *Lagenorhynchus albirostris*. 1, The disposition of the penis, mammary glands, and anus; 2, the penial muscles; 3, the organs from the ventral aspect; 4, dissection of verumontanum.

opening is also that of the lumen of the structure, for a crest projects into the cavity from the floor throughout its length. The crest becomes gradually reduced towards the blind end of the single sinus.

Cleland (*loc. cit.*) stated that in the white-beaked dolphin "there are four openings into the floor of the first part of the urethra. The two

upper are the openings of the vasa deferentia; and immediately beyond these are two larger openings distinct one from the other, and both leading up into a single sinus pocularis." Such a variation, it has been noted above, is also found in the porpoise, the cavity in both cases being a single one, but the opening single or double. The ridge, it will be noted, on the floor is more prominent in Lagenorhynchus than in Phocæna.

The verumontanum, in both the normal and the abnormal specimens, is a longitudinal ridge on the floor of the urethra. It begins near the base of the bladder as a double ridge on which the ureters open, fuses to a single ridge, and expands opposite the prostate gland to receive the openings just mentioned, and narrows again to gradually disappear in the urogenital duct. On either side of this latter narrow part the numerous openings of the prostate glands occur in rows.

The general structure and musculature of the penis are the same as those of the porpoise, and require no further special description. The urethra opens, as has been stated, in both the normal and the abnormal specimens, terminally by a horizontal slit. It will be seen from the drawings that the free part of the penis rapidly narrows, but it is occupied throughout its length by a single corpus cavernosum, which ends some little distance from its extremity. With regard to this, Cleland (*loc. cit.*) made the significant observation that "in the white-beaked dolphin the combined corpora cavernosa, about 2 ins. from the free extremity, are suddenly compressed as if by removal of more than half their substance on the ventral side, and then expand again to taper to the point." This is so like the formation of the penis of the porpoise as to give the impression that the function is essentially the same. Cleland added, "It is such an arrangement as will allow the slender end to be folded down on meeting with resistance in the erect condition"; but, as has been pointed out, the jointed end of the penis of the porpoise is the only part which gains access to the vagina, and it may be that this is the case also with reference to Lagenorhynchus.

Notes on the Male Organs of other Species of Delphinidæ.

A few notes may be added here with reference to one or two other species which were dissected in Dundee. In a fœtal beluga, *Delphinapterus* (*Beluga*) *leucas*, about 12 ins. long, the penis was found to be rounded and tapering as in Lagenorhynchus. The verumontanum presented three openings, the vasa deferentia and the uterus masculinus. The latter is interesting, as distally it is stretched out into a flattened cavity (fig. 11). A fœtal narwhal (*Monodon monoceros*) was dissected, and the general disposition of the organs is shown in fig. 12, and from these it will be noted that the penis has a similar shape to those already described.

From the drawings in my possession the conditions in the dolphin (*Delphinus delphis*) appear to be fundamentally different. The penis is

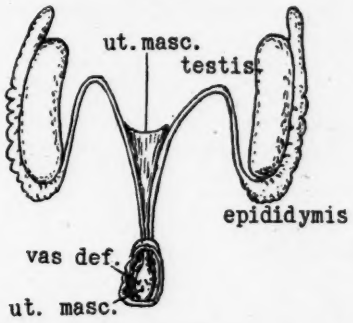


FIG. 11.—The vasa deferentia and uterus masculinus of a fœtal beluga (*Delphinapterus leucas*).

evidently short and only slightly tapering (fig. 13). There is some evidence in the drawing of a change in the corpus cavernosum near the extremity similar to that described in the other species, but it would be necessary to

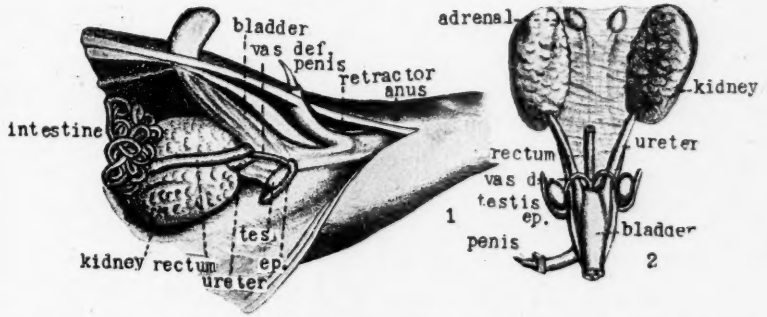


FIG. 12.—1, A general dissection of a fœtal narwhal (*Monodon monoceros*) to show disposition of male organs; 2, the reproductive organs in ventral view. It will be noted that the bladder has been reflected backwards.

examine the species afresh to establish the point. The pouch is evidently proportionally short. There appear to be only two openings on the verumontanum, those of the two vasa deferentia The two openings are approximated into a crescent-shaped aperture leading into the separate vasa

deferentia, a narrow septum separating the terminal portions of the ducts, in which no trace of a uterus masculinus was found (fig. 14).

The penis of *Kogia breviceps* was described by Benham,[1] and it is evident that in it the corpus cavernosum suffers a reduction in size anteriorly,

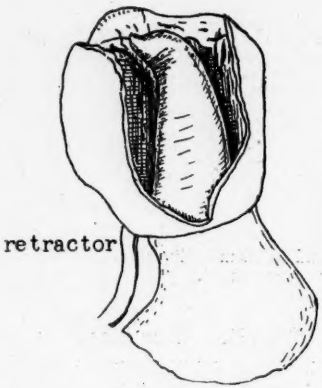


FIG. 13.—Penis and preputial pouch of dolphin (*Delphinus delphis*).

FIG. 14.—The verumontanum of the dolphin.

becoming circular in section. This modification of the preputial part of the penis appears therefore to be general in whales.

GENERAL CONSIDERATION.

A. *Morphological.*

The reproductive organs of the Cetacea, so far as may be gathered from a consideration of the foregoing species, are of a generalised mammalian type, with special modifications connected with the pelagic life of the group. It is in connexion with the muscles relating to these organs that the pelvic bone has been preserved, and it is worth noting that it is smaller in the female than in the male.

It would be interesting to know to what extent the spermathecal recess is developed in the females of other species.

The separation of the penis of the porpoise into a special copulatory jointed to a non-copulatory part is a remarkable modification, and has been led up to, doubtless, by the penis becoming narrow anteriorly, as is the case

[1] 1901, *Proc. Zool. Soc.* (ii.), p. 123.

in so many toothed whales. There is no true glans, but it appears to be the fact, from a consideration of the structure of the clitoris, that the glans has been secondarily invaded by the corpus cavernosum.

In other respects the organs do not arouse a great deal of interest. The absence of Cowper's glands is certainly worthy of remark, for they are so constantly present in mammalia. They are absent also in Arctoid Carnivora. The absence of seminal vesicles is not of such moment, for it is a feature which is not uncommon in primitive types, as monotremes, marsupials, the sloth, and in seals and other Carnivora. It is not necessary, in the case of a group so modified as the Cetacea, to make a point as to the abdominal position of the testes.

The uterus masculinus is generally present as a single tube lying between the terminal ends of the vasa deferentia. The opening of this single sinus pocularis is usually one in the fœtal stage, but may be, and usually is, double in the adult. The condition of the sinus in association with independent Müllerian ducts in an abnormal male Lagenorhynchus is noteworthy. A sinus pocularis does not appear to be represented in primitive mammals, and its presence here in a reduced condition is thus of interest. But the question of its homology will have to be reconsidered.

The preputial pouch must be considered also as a primitive feature, and in relation to the condition of life of the Cetacea its presence is plain. From the fact that the penis is everted in some of the (and especially in the younger) fœtuses, it may be held to be secondary in origin. Associated with the pouch is a retractor ligament which in some cases appears to be more or less muscular in composition. In the porpoise it is a strong double elastic ligament extending from the rectum to the preputial pouch.

Both the pouch and the retractor muscle are represented in the female. The muscle is especially interesting, for it originates in a tendon, expands above the clitoris into a muscle, and narrows again to be inserted into the prepuce. The presence of a retractor may also be said to be a primitive feature.

The erector penis and the accelerator muscles are strongly developed in the male. The erector clitoridis, though small in comparison with the corresponding muscle of the male, is well developed, and the sphincter vaginæ (accelerator) is also a prominent muscle encircling the opening of the vagina. It comes into association with the erector and also with the levator ani. Sebaceous glands occur in the preputial pouch in both sexes, and their secretion in the case of the male is always evident.

B. *Physiological.*

It is more than probable that the act of micturition necessitates the protrusion of the anterior end of the penis from the preputial pouch. If this be the case, it means that the penis is erected to some degree. The bladder is strong and muscular, and no doubt can be completely emptied by the contraction of its muscular wall, and it is evident that this is followed by the long urethral duct being emptied by the action of the accelerator muscle.

In the case of the female there appears to be little doubt that urination is accompanied by an erection of the clitoris. As will be seen from figs. 1 and 2, the urethral duct, in the resting condition, points towards the posterior wall of the entrance into the vagina. The corpus cavernosum of the clitoris, as will be seen from fig. 1, is so constructed and disposed as to make it apparent that during erection the main part of it will be straightened, and this will have the effect of bending forwards and downwards the glans, thus bringing the opening of the urethra to a ventral position and directed outwards. At the same time the distension of the whole structure will result in the clitoris and the urethral opening being carried downwards. In this case it is not necessary to consider that any muscular effort is required except that of the bladder, but the terminal end of the urethra is enclosed in the sphincter vaginæ.

It has been suggested that the males frequent the inshore waters during the pairing season, and that the females enter the region as they come into season. Whether this be the case or not, it is evident that the migration is due to a periodical development of the gonads. During the summer porpoises are very common inshore, and they may frequently be seen swimming in pairs. Mennell and Perkins[1] refer to their "grotesque gambols on the surface of the water, especially during the herring season."

As has been stated, we have not yet come across a female which has been in copulation. But the attempt has been made to indicate how the act is accomplished in pelagic conditions, and what is said about the porpoise will apply in the main to the other Cetacea.[2] It is not necessary to repeat that description here, but a few words may be added as to the physiological changes which are more or less specialised in the porpoise and other Cetacea.

The vulva is prepared for the reception of the penis by the descent of the erected clitoris, the glans being rotated forwards. This puts the

[1] *Trans. Tyneside Field Club*, vol. vi., 1863–64.

[2] A summary of the scanty knowledge we possess is given on p. 219 of Millar's *Mammalia of Great Britain and Ireland*, vol. iii.

retractor clitoridis on the stretch, and this muscle may be said to join synchronously in the pulsations of the erector muscle.

The erection of the penis similarly brings about an elongation of the retractor ligament. It is apparently a gradual process, for complete erection appears to be postponed until copulation. When the penis is protruded the free end of the copulatory part enters the vulva and is directed into the vaginal opening distending the sphincter muscle. The whole of the copulatory part of the penis gains access to the vagina; the main body of the penis, culminating as it does in a prominent knob, only reaches the vulva where it abuts against the clitoris.

It has been noted above that in the case of two of the females a discharge was seen to be issuing from the narrow opening of the vagina. The exact nature of the glands which give rise to this has not yet been determined. It is probable that in association therewith the sphincter muscle of the vagina is thrown into a pulsation. If this takes place, as is more than likely, on the withdrawal of the penis, water may thus be introduced into the vagina, but the folds which guard the spermathecal recess will obviate any danger of the ejaculate being lost.

The levator ani in both cases may be said to help by keeping the parts taut.

The presumption that erection and discharge may take place as a result of drowning raises interesting physiological questions as to the factors. It cannot be said to be the result of direct stimulation of either of the centres. It seems to be due to want of oxygen or perhaps more probably to the effects of the general fatigue produced by struggling. An examination of other cases of the kind, in relation to this, may point to the cause.

Notes on Literature.

The peculiar disposition of the corpus cavernosum in the porpoise does not appear to have been described by any of the many authors who have examined the male organs of this species. The fact that there is no true glans has generally been noted. Beauregard and Boulart,[1] and also Daudt[2] have found, as I have found, that the preputial pouch is a secondary formation; but it is not necessary because of that to call the pouch pseudo-preputial as Daudt proposes.

The musculature in the case of the Greenland whale has been described by Struthers,[3] and in the case of the Grampus by Turner.[4]

[1] *Journ. d. l'Anatomie et de la Physiologie*, 18 ann., 1882.
[2] *Jenaische Zeitsch.*, Bd. xxxii., 1898.
[3] *Journ. Anat. and Phys.*, vol. xv., 1881.
[4] *Ibid.*, vol. xxvi., 1892.

Daudt failed to see the preputial pouch in the female porpoise, but indicated its presence in other toothed whales, Beluga and Hyperoodon, and he observed it, as others have done, in Balænoptera. He appears, however, in some cases, to have confused the body of the clitoris with the preputium.

Daudt has described the two folds which form the spermathecal recess in the porpoise, but without indicating their significance, and his figure does not clearly indicate their disposition. Watson and Young[1] found eight such folds in Beluga, and Daudt said there were ten, the cervix being the first of the series. With reference to this genus I can now say that the penis is pointed, the free portion being spindle-shaped. Sections of the penis of a fœtal Beluga measuring 17·5 cm. show that, as in Lagenorynchus, the corpus cavernosum suddenly becomes reduced in size and rounded in section. This reduced part of the corpus cavernosum springs from the dorsal region of the body, and extends near to the extremity. The penis, as in the porpoise and as in Lagenorynchus, is therefore resolved into a proximal fixed part and a distal flexible part. This is associated in the case of the Beluga female with a succession of structures which resemble the cervix in structure, and probably in function. With their development the cervix has disappeared as such, and is probably represented by the small fold at the uterine end of the vagina which marks the first of the series. Daudt found that in Hyperoodon there were four to five such folds, and in Balænoptera there were about ten. There seems to be some degree of variation in Balænoptera with regard to the number and the disposition of the folds, for in the species described by Beauregard and Boulart the number is less than that described by Daudt, and the lower folds appear to undergo some degree of anastomosis.

The Female Organs of the Greenland Whale (Balæna mysticetus).

Since the foregoing was written I have examined the female organs of a fœtus, measuring 41 cm., of the Greenland whale. This specimen was presented to the Natural History Society of Newcastle in 1835 by T. R. Batsom, and is preserved in the Hancock Museum.

So far as I know, the organs have not been described with reference to this species, and they present some features of interest. The vulva is quite small, measuring only 5 mm. in diameter, and is rounded in shape. The anal opening is situated about 5 mm. posteriorly, and the minute openings of the mammary glands are placed on either side but somewhat

[1] *Trans. Roy. Soc. Edinburgh*, vol. xxix., 1879.

anterior to the vulva. The vulva was found to be occupied by a clitoris, which is elongated and coiled. It is thus so far like the penis in shape as to indicate that the penis is long and tapering, as it is in so many of the Cetacea.[1] The clitoris springs from the base of a shallow preputial pouch and it is evident, therefore, that it represents, as in the porpoise, the free preputial part of the penis. The preputial pouch completely surrounds the clitoris, and is continued by folds with the eminence on which the urethra opens. Beyond the vulva there is a long, roomy vagina. Near the vulva the wall of the vagina is thrown into longitudinal folds, and these can be traced, especially on the dorsal side, along rather more than

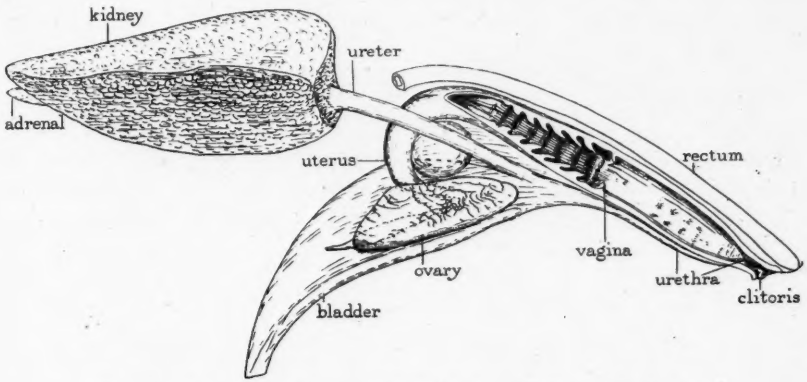


FIG. 15.—The urino-genital organs of a female fœtus of the Greenland whale, measuring 41 cm. (×2.)

half its length. Otherwise the lower part of the vagina has a smooth wall in which pit-like depressions occur at intervals. The upper part of the vagina is occupied by a series of transverse folds similar to those which have been described in the species mentioned above. There are seven complete rings, a trace of an eighth at the upper end of the series, and at the lower end two incomplete folds on the right and left sides. They are traversed by longitudinal folds, which are especially well marked at the upper end and are almost absent from the incomplete folds at the lower end.

As in the other cases in which such folds have been found, the condition is accompanied by the absence of the cervix. If it be the fact, as the structure certainly indicates, that the cervix has disappeared, we have in these cases the development of a series of folds which have replaced the

[1] Struthers, *Journ. Anat. and Phys.*, vol. xv., 1881.

cervix in function. The vagina has thus been peculiarly modified in a large number of the Cetacea, in a manner which appears to be without parallel in other Mammalia, and is even strikingly different from the conditions in the porpoise.

In the light of the foregoing description it may be suggested that they have a double function. The penis will have to pass through a number of the folds at least, and it is probable, therefore, that they have been developed for the purpose of promoting the discharge. It will be noted that the folds are directed downwards and they are highly muscular. It is possible, therefore, that the folds are expanded and contracted, and depressed and raised, and such movements would have the effect of sending the spermatic fluid upwards, to and towards the uterus. Even in the case of the porpoise it is quite possible that the two folds are thrown into similar movements.

The uterus a short distance above the folds divides into the two horns, which are bent ventrally and backwards. The Fallopian tube presents a few folds, and, like the large funnel into which it opens, is directed forwards. The ovary is large, and it is beset with numerous furrows as it is in Balænoptera. The broad ligament is occupied on each side by a round fat body, such as was found by Beauregard and Boulart in Balænoptera.

THE PRIMORDIAL CRANIUM OF ERINACEUS EUROPÆUS.

By EDWARD FAWCETT, M.D., *Professor of Anatomy in the University of Bristol.*[1]

THE specimen from which the model illustrating this communication was made I owe to the kindness of Prof. J. P. Hill, of University College, London. In total length it was 25 mm., and was cut into sections of 25 microns thick, stained before cutting with alum-cochineal, and then on the slide with Mallory's triple connective-tissue stain.

Being an Insectivore, it was thought of interest to examine it in detail and compare it with the mole.

The cranium may be divided into an axial and an appendicular, or a neural and a visceral part, neither division being quite satisfactory. The former is that more particularly associated with the encephalon, the latter the skeletal basis of the visceral arches. We may therefore consider *seriatim* the neural chondrocranium, the visceral cartilaginous skeleton, and finally the bones where they are found.

THE PRIMORDIAL NEURAL CRANIUM.[2]

This is perhaps most conveniently considered as consisting of the following parts, viz.:—

1. A central stem, to which are appended, at more or less constant positions,
2. Appendages to the central stem;
3. Lateral structures;
4. Commissures binding these lateral structures together;
5. Dorsal structures, *i.e.* structures which lie dorsal to the encephalon and form a cartilaginous roof to the cavum cranii.

1. THE CENTRAL STEM. (Pls. 1, 2.)

The central stem stretches at this stage uninterruptedly from the anterior margin of the foramen magnum to the tip of the nose. As far

[1] The expenses of this research were largely defrayed by a grant from the University of Bristol Colston Society's research fund.

[2] In order to justify this mode of description, several plates are appended. They represent the condition as seen in the 11-mm. mole, 12- and 17-mm. Tatusia, and ?19-mm *Bos taurus*.

forwards as the nasal capsule it is much wider than deep; but once it has become included within the nasal capsule, its depth suddenly increases; its width at the same time diminishes, so that from now onwards as nasal septum the depth of the central stem is greater than its width (Pl. 5).

Constituent Parts of the Central Stem.—Morphologically the central stem appears to be made up of the following parts from behind forwards, viz.: (i.) a part in some relation to the notochord—the *pars chordalis* (Pls. 1, 2); (ii.) a part related of the hypophysis and its stomodæal duct—the *pars trabecularis* (Pls. 1, 2); and (iii.) a part which, lying between the optic foramina, then as traced forwards between the orbital cavities, and finally within the nasal capsule as the nasal septum, may be alluded to as a whole as the *interorbito-nasal septum* or *pars interorbito-nasalis* (Pls. 1, 2).

In Talpa (Pl. 22), and in Tatusia (Pls. 16, 17, 18) and Cavia, these parts chondrify independently of one another. Whether they do so or not in Erinaceus has not yet been determined, for want of material; but it is most probable that they do. In the calf (Pl. 13) and man (Pls. 19, 20) the pars chordalis chondrifies independently of the pars trabecularis, but I do not know if the latter is independent of the interorbito-nasal septum.

At the stage now being described, as all these parts are fused together and no histological difference can be made out anywhere in the central stem, their sites of union can only be surmised.

Detailed Description of the Central Stem.—The *pars chordalis* (Pls. 1, 2) may be looked upon as a quadrilateral plate, wide and concave behind as it forms the anterior boundary of the foramen magnum. The postero-lateral angles are fused with the exoccipitals, only the hypoglossal canal indicating any demarcation between the two, and there is no developmental distinction since the exoccipital is a direct outgrowth from the chordal plate; but, for later convenience, ossification taking place as it does independently in the exoccipital and extending medially towards the basi-occipital centre, one may speak of this cartilage as the exoccipital.

The lateral margins of the chordal plate are partly free where they look towards the foramen jugulare and partly directly fused with the cochlear capsule; anteriorly the chordal plate is fused with the pars trabecularis, and an imaginary line drawn transversely through the middle of the cochlear capsule may be taken as indicating the site of fusion between the pars chordalis and the pars trabecularis.

The Pars trabecularis (Pls. 1, 2).—This, assuming its commencement to be as stated above, is of large size, and very slightly hollowed to receive from above the hypophysis. It may be regarded as a quadrilateral plate with an imaginary posterior border at the aforesaid junction with the pars

chordalis. Its anterior boundary is also an imaginary one, formed by drawing a line transversely through the central stem immediately behind the hinder root of the ala orbitalis (Pl. 1). From its postero-lateral angles on each side are given off the following parts: from behind forwards, first the *posterior trabeculo-cochlear commissure*, fused with the *chordo-cochlear commissure* (Pl. 1), next the *anterior trabeculo-cochlear commissure* (Pl. 1) which runs back to the lateral side of the apex of the cochlear capsule (Pl. 1). Between the anterior and posterior trabeculo-cochlear commissures the carotid foramen (Pls. 1, 2) is found. Then follows the *ala temporalis* (Pls. 1, 2), which at this stage is fused at its root with the anterior trabeculo-cochlear commissure. The lateral border of the pars trabecularis is now free and forms the medial margin of the anterior segment of the *spheno-parietal foramen* or *fontanelle* (Pls. 1, 2). In the centre of the pars trabecularis a large circular foramen is met with; this transmits the stomodæal duct and is the *cranio-pharyngeal canal* (Pls. 1, 2). It is to be noted that the main mass of the hypophysis always lies behind this foramen.

Two cartilages lie below the pars trabecularis, and are developed independently of the neural chondrocranium. These are the cartilaginous masses developed in connection with the pterygoid bone (Pl. 2). Each is a somewhat ovoidal mass whose long axis is directed sagittally. Each is placed infero-medial to the processus pterygoideus of the ala temporalis and separated from it by the vidian (parabasal) nerve. No pterygoid bone is developed at this stage in connection with it, but on its supero-lateral aspect a dense crescentic mass of connective tissue, which occupies the position one usually associates with the pterygoid bone, is found. This mass, too, lies immediately behind the *os palatinum*. The mass of cartilage just described has on its outer side the tendon of the tensor palati muscle, and is evidently the cartilage of the *hamulus*.

The Pars interorbito-nasalis (Pls. 1, 2, 5, 6).—This in Erinaceus is of quite unusual width, and receives at its sides the two roots of the ala orbitalis, between which the optic foramen lies on each side. Perhaps the hinder root or limb of the ala orbitalis is really connected with the pars interorbito-nasalis through the *ala hypochiasmata* (Pl. 2), but that could not be determined at this stage. Free of the two limbs of the ala orbitalis, the lateral free margins of the pars interorbito-nasalis now form the medial boundary on each side of the *orbito-nasal fissure* (Pl. 1), then this interorbito-nasal septum becomes included within the nasal septum. The nasal septum will be described in detail with the nasal capsule.

2. Structures appended to each side of the Central Stem.

From behind forwards are:—

(1) The exoccipital cartilage or pila occipitalis;
(2) The auditory capsule;
(3) The ala temporalis;
(4) The ala hypochiasmata and the ala orbitalis;
(5) The lateral nasal capsule.

(1) *The Exoccipital Cartilages* (Pls. 1, 2).

Each may be taken as extending from an imaginary line drawn through the medial margin of the hypoglossal canal in an antero-posterior direction. Each passes backwards and outwards at first, having a free antero-lateral border which forms the hinder boundary of the *foramen jugulare* (Pl. 2),

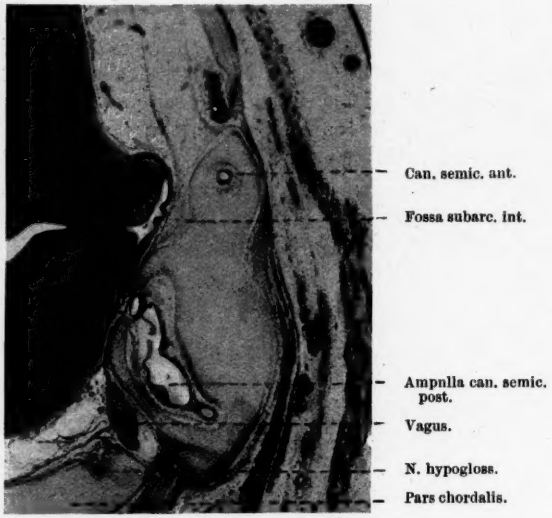


Fig. 1.—*Erinaceus europæus.* All the sections are coronal ones.

and a postero-medial border which forms the lateral boundary of the primary *foramen magnum* (Pls. 1, 2). Beyond the lateral limit of the foramen jugulare, the exoccipital cartilage is projected under the pars canalicularis of the auditory capsule in the form of lamina—the *lamina alaris* (Pl. 2), which, for the most part separated by a narrow fissure—the

recessus supra-alaris (Pl. 1 and fig. 3)—from the auditory capsule, is terminally fused with that capsule, so that the fissure above mentioned can only be seen from within, and that only after removal of the lateral sinus. The recessus supra-alaris is itself occupied by dense cellular tissue. At its anterior extremity the lamina alaris is fused with the infero-lateral margin of the pars canalicularis of the auditory capsule, and it projects sufficiently below that region to be recognisable externally as a *processus paracondlyoideus* (Pl. 2), to whose under surface the musculus rectus capitis lateralis is attached (fig. 3).

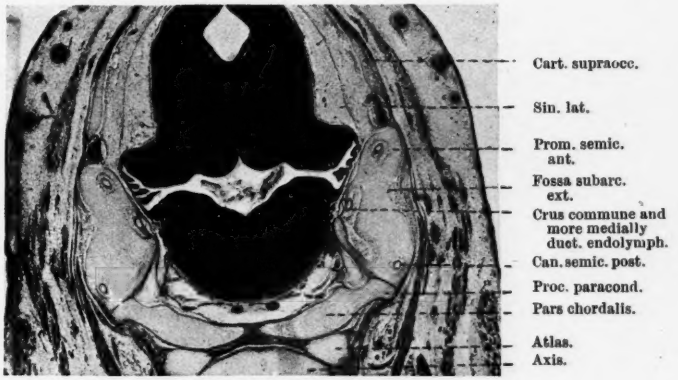


FIG. 2.—*Erinaceus europæus.*

In a coronal section of the auditory capsule (figs. 1, 2) above the point of fusion with the processus paracondyloideus one can see the posterior semicircular canal. Before the hindmost limit of this canal is reached, the exoccipital cartilage has once more freed itself from the auditory capsule and is thus separated from it by a narrow fissure, the *fissura occipito-capsularis inferior* (Pls. 3, 4, 7, 8), and the paracondyloid process has come to an end. This fissure is of comparatively short extent, because the ex-occipital cartilage once more fuses with the pars canalicularis, but this time with the postero-medial aspect of the posterior pole of that capsule, so that a recess is produced between the two, which is visible from the exterior. The region of fusion between the posterior pole of the pars canalicularis of the auditory capsule and the exoccipital cartilage may be termed the *occipito-capsular commissure* (Pls. 7, 8). Here the exoccipital cartilage comes obliquely to an end (Pls. 4, 8). Its medial margin forms a consider-able part of the lateral boundary of the primary foramen magnum.

(2) *The Auditory Capsule* (Pls. 1, 2, 7, 8).

This structure taken as a whole may be described as a truncated three-sided pyramid, placed very nearly at right angles with the central stem, but with a slight inclination forwards. Together with the pars chordalis of the central stem, the auditory capsules form the floor of that part of the cavum cranii which lodges the parts derived from the hind brain—a part which is as large as the rest of the *cavum cranii*.

The auditory capsule may be regarded as consisting of two main parts:

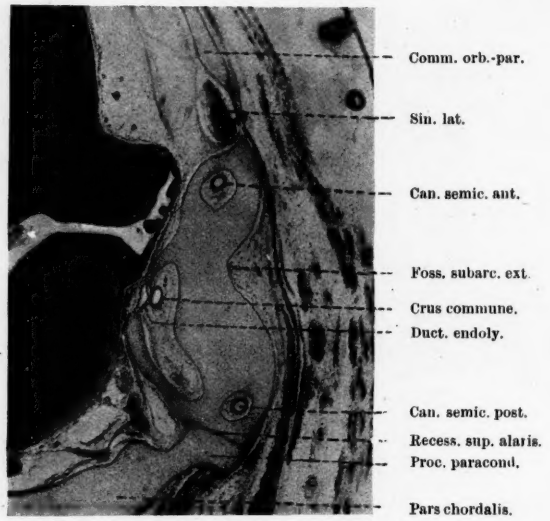


FIG. 3.—*Erinaceus europæus.*

one, more posterior, forming the basal part of the pyramid, and which, because it contains in its interior the semicircular canals, is termed the *pars canalicularis* (Pls. 1, 2, 3, 4, 7, 8); the other, which is directed forwards and medialwards, because it contains mainly the cochlea is the *pars cochlearis* (Pls. 1, 2, 7). The small size of this latter part, and especially that which actually contains the membranous cochlea, is very striking.

The auditory capsule is moored to other parts of the neural chondrocranium at certain precise spots; thus, the pars cochlearis is fused along the whole of its medial border to the central stem (Pls. 1, 7), and no basicochlear fissure is present at this stage at all events, in which respect

Erinaceus differs markedly from Talpa (Pl. 9). The posterior trabeculo-cochlear and the chordo-cochlear commissures have fused together to form a common commissure just lateral to the apex of the cochlear capsule. The anterior trabeculo-cochlear commissure connects the cochlea with the postero-lateral angle of the pars trabecularis, and at the same time this commissure is fused with the proximal portion of the ala temporalis (Pls. 1, 2, 7). The pars canalicularis inferiorly is fused with the par-occipital process of the exoccipital (Pls. 7, 8), and again, by the inner aspect of its posterior pole, is fused with the anterior edge of the upper end of that cartilage (Pls. 7, 8). From the anterior half of the upper border of the pars canalicularis there projects in an upward direction a thin plate, the *parietal plate* (Pls. 3, 7, 8). This, by its anterior margin, is fused with the *orbito-parietal commissure* (Pl. 3), which connects the parietal plate thus with the ala orbitalis. The posterior margin of the parietal plate is fused with the supra-occipital cartilage of the corresponding side (Pls. 3, 7, 8), but the under margin of the latter cartilage is separated from the hinder half of the upper margin of the pars canalicularis by a well-marked fissure—the *fissura occipito-capsularis superior* (Pls. 3, 7, 8), a fissure which at its anterior end transmits the lateral jugular vein and is in itself blocked up by the down-coursing lateral sinus. In the intervals between the various commissures mooring the auditory capsule to neighbouring parts of the chondrocranium, vacuities are met with; thus, antero-lateral to both pars canalicularis and pars cochlearis, the spheno-parietal fontanelle is seen (Pls. 1, 2, 3, 4, 7); anterior to the apex cochleæ the carotid foramen (foramen caroticum) (Pls. 1, 3, 7). Infero-medial to the capsule one sees the jugular foramen continued laterally as a recessus supra-alaris (Pls. 1, 2, 7, 8). Finally, above the posterior pole of the pars canalicularis, between the hinder half of the upper margin of the pars canalicularis and the anterior process of supra-occipital cartilage, is the superior occipito-capsular fissure (Pls. 3, 4, 7, 8).

If we now examine in detail the parts of the auditory capsule, commencing with the pars canalicularis, we find that—

The Pars canalicularis represents the basal part of the capsule (Pls. 1, 2, 3, 4, 7, 8). It contains in its interior the utricle and the semicircular canals; it owes much of its external form to its contents, as we shall see later. For descriptive purposes we may regard this region as having four surfaces, which from their direction may be termed lateral, anterior, medial, and inferior.

The lateral surface (Pls. 3, 4, 8) is irregularly quadrilateral, having an anterior, a superior, a posterior, and an inferior border. The anterior border is somewhat irregular in outline. Commencing above, one notices

a slight projection—the *tegmen tympani* (Pl. 3)—which, compared with that in a much younger stage in Talpa, is very small; below this there is a broad sulcus, and below this a notch which is the outer end of the *fossa incundis* (Pl. 3), in which, in the model, the *processus posterior* of the incus cartilage is observed lying. Below this a projection, the *crista parotica* (Pl. 3), is met with, and from the lower part of this there projects in a downward and a forward direction the *processus styloideus* (Pl. 3). Behind and below the root of the processus styloideus there is a broad notch, through which the facial nerve appears. This notch is in the position of the *primary stylo-mastoid foramen*, and it may also be taken as at the anterior limit of the inferior border of the lateral surface of the pars canalicularis.

The inferior border, commencing as said at the hinder part of the site of attachment of the root of the processus styloideus, is first notched by the facial nerve, behind which it is notched by the stapedius muscle to form the *incisura stapedii*; behind, this border is fused with the outer edge of the *processus paracondyloideus* of the exoccipital, a slight groove (Pl. 8), seen from the lateral aspect, separating the two superficially.

The posterior border (Pl. 8) stretches from the hindmost part of the site of fusion of the aforesaid parts and runs almost vertically upwards to reach the posterior pole of the auditory capsule or *cupula posterior*. In this part of its course it is separated from the exoccipital cartilage by a narrow fissure—the *fissura occipito-capsularis inferior* (Pls. 3, 4, 7, 8). At the posterior pole the pars canalicularis is fused with the exoccipital cartilage (Pls. 7, 8).

The superior border (Pls. 3, 4, 7, 8) stretches from the posterior pole in an arched fashion as far forward as the root of the tegmen tympani. In its hinder part it is free and forms the lower boundary of the superior occipito-capsular fissure, whilst in its anterior half the superior border gives origin to the parietal plate, which rises vertically here from it. Both this border and the posterior one are rounded, each being formed by the bulging of the contained semicircular canal, the former by the superior v. anterior; the latter by the posterior semicircular canal.

The Surfaces of the Pars canalicularis.—The *lateral* surface (Pls. 3, 4, 8) is quadrilateral; at its upper margin and for some distance below is a semi-cylindrical swelling reaching practically the whole length of the upper part of the surface, and caused by the superior v. anterior semicircular canal, therefore called the *prominentia semicircularis, superior* or *anterior* (Pls. 3, 7). Along the posterior border of the surface the *prominentia semicircularis posterior* (Pls. 3, 7) is met with. This reaches from the posterior pole to the neighbourhood of the paracondyloid process of the exoccipital, and from near the lower end of this prominence another of

considerable width runs upwards and forwards towards the upper end of the crista parotica and is the *prominentia semicircularis lateralis* (Pls. 3, 8), which is caused by the lateral semicircular canal. Between this prominence and the prominentia semicircularis superior v. anterior is a large hollow, which may be termed the *fossa subarcuata superior externa* (Pls. 3, 9). This fossa is occupied by connective tissue. No opercular process is developed in connection with the lateral surface, in which respect it is unlike that of Talpa (Pl. 10).

The anterior surface (Pl. 7A) is bounded, in the main, laterally by the prominent crista parotica. It commences above, below the tegmen tympani, is below this grooved by the facial nerve—*sulcus facialis*,—and further down, in addition, by the stapedius muscle. As a matter of fact, a large part of the fossa stapedii, which ends below at the *incisura musculi stapedii*, lodges the stapedius muscle just below the point where the facial nerve turns forward and round the outer side of the root of the processus styloideus.

The medial surface (Pls. 1, 7; figs. 1, 2, 3) is next in point of size to the lateral surface. It is inclined a little upwards and somewhat towards the middle line. It shows just above its middle a fairly well-marked depression, surmounted by the *prominentia semicircularis anterior*. This hollow is the *fossa subarcuata anterior interna*. It contains loose connective tissue, and at some distance from it is the floccular part of the cerebellum, which therefore at this stage does not occupy it. Below this fossa is a large somewhat oval vacuity which leads into the interior of the pars canalicularis and in the recent condition is occupied by the *crus commune* of the labyrinth and by the *ductus endolymphaticus* (fig. 3). This, when reduced in size, as it doubtless is at a later stage, becomes the *foramen endolymphaticum* aquæductus vestibuli (Pls. 1, 7) and conducts the *ductus endolymphaticus*. Below this vacuity the inferior border of the medial surface is seen. It is rounded, and at its anterior part somewhat prominent, forming here the *prominentia utriculo-ampullaris posterior*. The upper border of the medial surface is rounded for the most part and formed by the prominentia semicircularis anterior (fig. 1). This ends below the anterior part of the spring of the parietal plate in a prominence, the *prominentia utriculo-ampullaris anterior* (Pls. 1, 7).

The *inferior surface* (Pl. 7; figs. 1, 2, 3) might also be termed the infero-medial surface, because it is to a large extent inclined towards the cavum cranii. It forms the roof of the *recessus supra-alaris* and to a slight extent that of the *foramen jugulare*. It is hidden from view by the lateral sinus when that is in position. At its most inferior and lateral part it is fused with the upper aspect of the lateral part of the paracondyloid process. Immediately beneath this surface in the recent

condition the vagus, glossopharyngeal, and accessory nerves are seen (fig. 1), and the auricular branch of the vagus is given off in this region. A slight *fossa subarcuata posterior* (Pl. 7; figs. 1, 3) is present.

The Pars cochlearis (Pls. 1, 2, 7).—This may be divided into a cochlear and a vestibular segment (Voit). These two segments contain respectively the cochlear duct and the saccule. The "vestibular" segment is characterised by the presence of a number of foramina which open into it from the exterior; thus, on the lateral aspect, the *fenestra vestibuli* (ovalis), closed by the foot of the stapes, is seen. On the inferior aspect a large vacuity, the common opening of the *fenestra cochleæ* (rotunda) and foramen perilymphaticum (*aquæductus cochleæ*) are met with. These

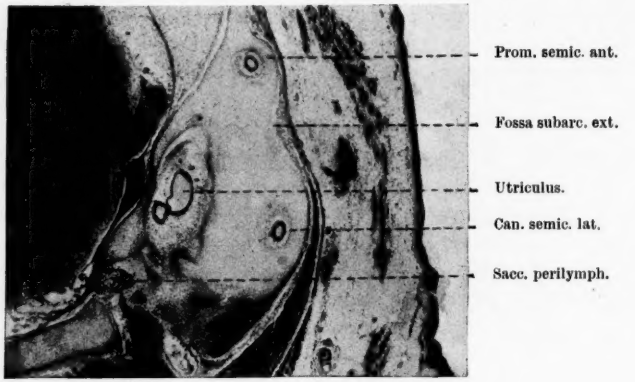


FIG. 4.—*Erinaceus europæus.*

two components are beginning to be separated from one another by a spur of cartilage growing from the posterior wall of the common vacuity towards the anterior wall; but when complete separation takes place (if indeed it do) I know not. The part of the vacuity destined to become the fenestra cochleæ is closed by a dense sheet of connective tissue, evidently the primordium of the secondary tympanic membrane, whilst that part which will become foramen perilymphaticum (aquæductus cochleæ) transmits veins from the cochlea and the ductus perilymphaticus, which latter at this stage is quite solid (fig. 4). The median wall of the "vestibular" segment of the pars cochlearis shows the *internal auditory meatus* (Pls. 1, 7), which has already become divided up into an upper and a lower part by a *crista falciformis* (Pls. 1, 7; fig. 5). The upper part is divided into an anterior foramen for the

facial nerve—*foramen faciale*, and a posterior part—the *foramen acusticum superius*, through which passes the upper branch of the vestibular division of the auditory nerve, whose branches run to the utricle, the ampullæ of the superior (anterior) and lateral semicircular canals, as well as to the upper and hinder part of the saccule. The lower segment of the internal auditory meatus is not at this stage divided up into secondary foramina. The lower division of the vestibular part of the auditory nerve supplying the lower and fore part of the

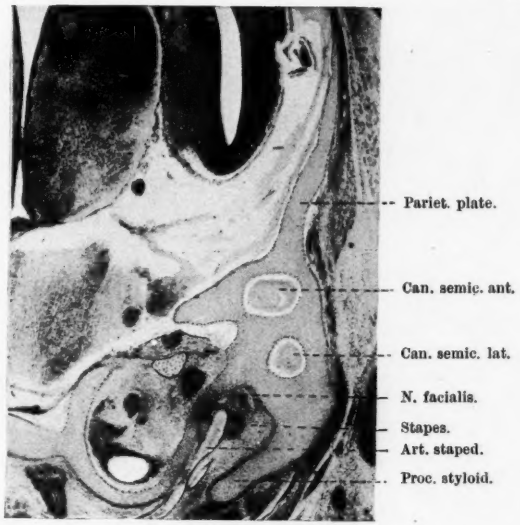


FIG. 5.—*Erinaceus europæus.*

saccule, and ampulla of the posterior semicircular canal, runs with the cochlear division of the auditory nerve through this lower segment of the internal auditory meatus.

The upper anterior wall of the *meatus auditorius internus* is formed by the *commissura suprafacialis* (Pls. 1, 3, 7)—a bridge of cartilage which stretches from the "cochlear" segment of the pars cochlearis backwards over the genu of the facial nerve to reach and fuse with the pars canalicularis. Before leaving the "vestibular" segment of the pars cochlearis, a word or two may be said regarding that surface of it directed towards the primary tympanic cavity. It is, as has already been mentioned, perforated by the fenestra vestibuli, which in the recent

condition is occupied by the foot of the stapes (Pl. 7A; fig. 5). Below this fenestra a large prominence—the *promontorium*—is met with, which indicates the position of the first turn of the cochlea. This is grooved about its middle, and in a vertical direction, by the stapedial artery. From the upper margin of the promontorium a sulcus runs forwards and medially towards the medial side of the apex cochleæ; this is the *sulcus caroticus*; it ends at the *foramen caroticum* (Pl. 7A). It corresponds for a considerable part of its extent with the *sulcus septalis*, a sulcus which corresponds itself with the *septum spirale* in the interior of the cochlear capsule.

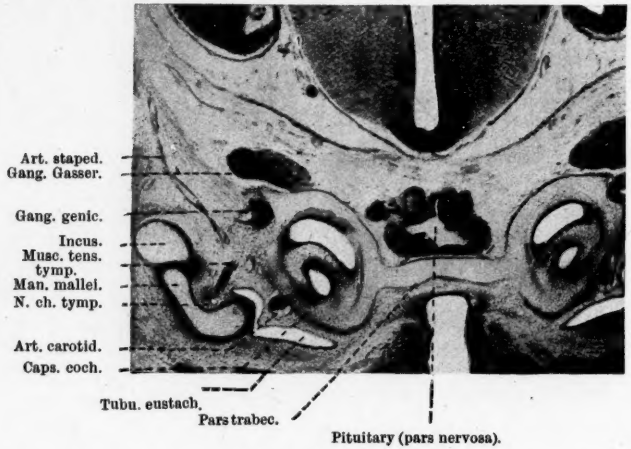


FIG. 6.—*Erinaceus europæus.*

The cochlear part of the pars cochlearis is very small (Pls. 1, 2, 7).[1] In this respect Erinaceus agrees much with Talpa (Pl. 9), and is in very striking contrast with the cat, in which the cochlear segment of the pars cochlearis is of enormous size; so large, in fact, are the cochlear capsules in the cat that they compress to a remarkable degree the chordal plate (Pl. 11), from which they are separated by a large basi-cochlear fissure, but they nearly meet in the middle line over that plate. The "cochlear" segment in Erinaceus has three surfaces, viz. a large *infero-lateral*, which is in continuity directly in a forward direction with the corresponding surface of the "vestibular" segment of the pars cochlearis, and

[1] I am informed by gamekeepers and by mole-catchers that the sense of hearing is poorly developed in the hedgehog.

is marked by the sulcus septalis and the sulcus caroticus, both of which tend to divide it into a lower medial part corresponding with the first coil of the cochlear duct, and an upper more lateral part which, projecting forward as the cupula or apex cochleæ, contains the remainder of the cochlear duct. Opposite the middle of the sulcus caroticus there is a deficiency (Pls. 2, 7A) in the cartilaginous wall of the cochlear segment evidently a "pressure" deficiency which is doubtless made good later. Over the outer side of the cupula near its basal part the great petrosal nerve descends, and after a very short course joins the carotid plexus of the sympathetic accompanying the carotid artery. The *superior* surface

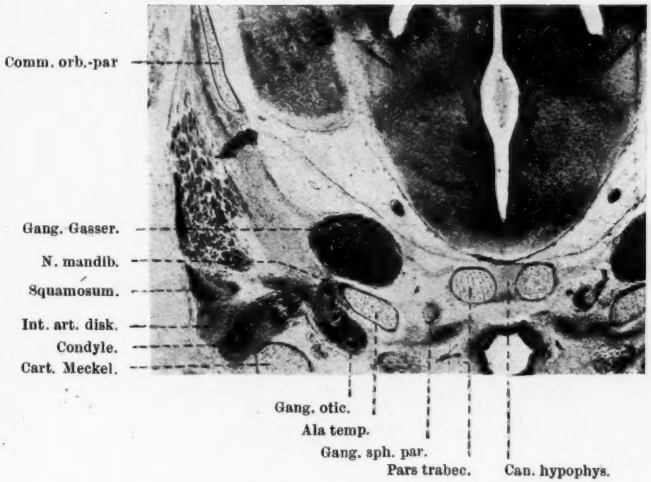


FIG. 7.—*Erinaceus europæus.*

of the "cochlear" segment is small and in part overlain by the Gasserian ganglion, more especially in its outer half and posteriorly, where the suprafacial commissure is being given off. The remainder of the superior surface is free and helps to join the floor of the cavum supra-cochleare of Voit. The *medial* surface is in relation with the hypophysis, a structure of enormous size in Erinaceus (fig. 6). This surface is fused in the whole of its length with the central stem, no basi-cochlear fissure being present (Pl. 7). From the region of the cupula the anterior trabeculo-cochlear commissure runs forwards and inwards on the latero-anterior aspect of the carotid foramen to join the stalk of the ala temporalis.

(3) *The Ala temporalis* (Pls. 1, 2, 3, 7).

This comparatively small cartilage springs from the postero-lateral angle of the pars trabecularis by a narrow stalk common to it and the anterior trabeculo-cochlear commissure. At first it runs directly outwards; but once the commissure above mentioned has left it, it begins to expand in a forward direction and forms a, for the most part, horizontally directed plate which breaks up into three processes (Pls. 1, 2, 3, 7), which are from

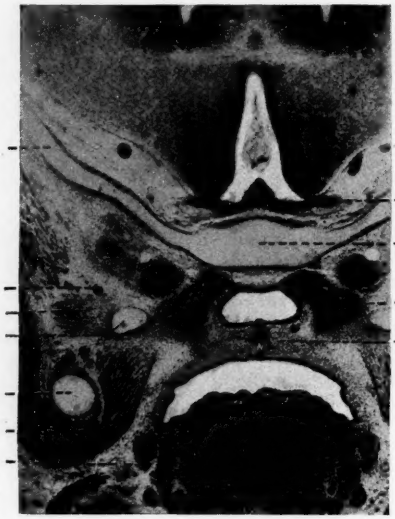


FIG. 8.—*Erinaceus europæus.*

behind forwards a postero-lateral, an antero-lateral, and an anterior. Between the postero-lateral and antero-lateral processes the mandibular division of the fifth nerve leaves the cranial cavity (fig. 7), the notch through which it goes being consequently the homologue of the foramen ovale, immediately below which is placed the otic ganglion. The antero-lateral process is especially the site of origin of the upper head of the pterygoideus externus muscle, which arises from its lower aspect and is coincident with it. The anterior process is the forward continuation of the medial thickened edge or *processus pterygoideus* of the ala temporalis; it juts forwards between the lower head of the pterygoideus externus and on its medial aspect the greater part of the pterygoideus internus (fig. 8).

(4) *The Ala orbitalis* (Pls. 1, 2, 3; fig. 8).

The ala orbitalis is a large triangular plate of cartilage whose base lies laterally and is included in the lateral structures enumerated above as entering into the neural chondrocranium. It forms part of the floor of the cavum cranii as well. By its anterior basal angle it is fused with a backwardly prolonged process from the frontal prominence of the pars intermedia of the lateral wall of the nasal capsule, forming the *sphenoethmoidal commissure* (Pls. 1, 3). Its posterior basal angle is prolonged backwards to fuse ultimately with the parietal plate and form the *orbito-*

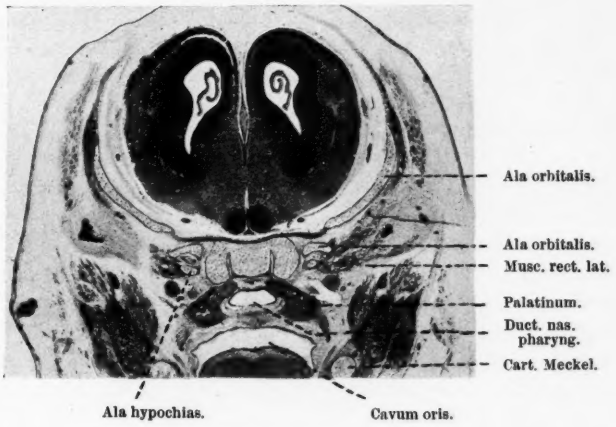


FIG. 9.—*Erinaceus europæus.*

parietal commissure (Pls. 1, 3). The apex of the ala orbitalis is directed towards the central stem (hinder part of pars orbito-nasalis); before reaching the central stem the apical region bifurcates into an anterior and a posterior branch (Pl. 1). The former reaches the central stem in front of the optic nerve; the latter reaches the central stem—? the ala hypochiasmata—behind the optic nerve, so that between the two limbs the optic foramen is formed. The optic foramen here is really a tunnel (fig. 9) whose floor is formed by the *ala hypochiasmata,* or at all events what corresponds with that structure in other mammals. The upper wall of the tunnel seems, so far as my experience goes, intrinsic to Erinaceus. It seems to give origin especially to the obliquus superior of the eyeball. The lower wall of the tunnel, the ala hypochiasmata proper, gives origin to the rectus system of muscles, especially the inferior and lateral recti. The anterior

border of the ala orbitalis is for the most part free, and forms the hinder boundary of the *orbito-nasal fissure* (Pls. 1, 2, 3), through which the nasal nerve enters the cranial cavity from the orbit to reach ultimately the cribriform plate of the ethmoid. Just lateral to the optic foramen a deep notch is found in the anterior free border of the ala orbitalis (Pls. 1, 3), but it does not transmit anything. The posterior border of the ala orbitalis is free, and forms at once the common anterior boundary of the spheno-parietal fontanelle and that segment of it which, lying anterior to the ala temporalis, is the representative of the sphenoidal or superior orbital fissure and foramen rotundum combined, through which run the maxillary and ophthalmic divisions of the fifth nerve, the third nerve, the sixth, as well as the fourth. It may here be mentioned that the maxillary division of the fifth nerve does not perforate the ala temporalis, so that a foramen rotundum is absent, as is the case in most mammals. The outer surface of the ala temporalis is marked by a horizontal sulcus in which the supraorbital artery lies, down to the level of which reaches the frontal bone.

The Ala hypochiasmata (Pls. 2, 3; fig. 9).—This has already been alluded to as probably the lower half of the optic tunnel, and is well marked in Erinaceus. It gives origin to the rectus system of muscles of the eyeball, and at this stage seems to be associated with the hinder branch of the apex of the ala orbitalis. How it develops in Erinaceus I know not, but in Tatusia novemcincta it is developed independently. Possibly that is its usual mode of development, and recently Kernan has shown this to be the case in man.

(5) *The Lateral Nasal Capsule.*

This, though truly a lateral appendage to the central stem, will be described with the nasal capsule.

3. Lateral Structures.

These are the ala orbitalis, the parietal plate, and the anterior process of the supraoccipital cartilage. *The ala orbitalis* has been fully described, and nothing more need be said concerning it.

The Parietal Plate (Pls. 3, 7, 8), already mentioned in connection with the pars canalicularis of the auditory capsule, is a very simple structure, and may be considered as a quadrilateral plate fixed by its lower border to the anterior half of the upper margin of the pars canalicularis of the auditory capsule (fig. 5). Its anterior margin is free, and helps to form the posterior boundary of the spheno-parietal fontanelle. Its superior margin is likewise free. Its superior margin forms the anterior boundary of the superior

occipito-capsular fissure. Its antero-superior angle is fused with the orbito-parietal commissure, whilst its postero-superior angle blends with the anterior process of the supraoccipital cartilage. It is covered laterally at this stage by the parietal bone, but only in its upper half. The lower half of its outer surface is covered by a thick layer of perichondrium, from which arises part of the temporal muscle.

The Supraoccipital Cartilage (Pls. 1, 3, 4, 7, 8).—This cartilage is of great interest in Erinaceus at this stage, because it perhaps gives us the key to the morphological history of what will later be alluded to under the name *tectum synoticum* or *tectum posterius*.

It may be described as a triangular plate whose apex is directed downwards towards the pole of the pars canalicularis of the auditory capsule (Pl. 8). Its anterior basal angle is fused with the postero-superior angle of the parietal plate, whilst the posterior basal angle stretches medially over the cavum cranii to meet its fellow in the middle line, fuse with it, and form the so-called tectum synoticum or tectum posterius, which in Erinaceus is very narrow. The under margin of the supraoccipital cartilage is free, and forms the upper boundary of the superior occipito-capsular fissure. The upper margin is free and somewhat irregular; whilst the lower margin, at first near the apex, connected by fibrous tissue with the oblique upper edge of the exoccipital cartilage and more medially for a short distance fused histologically with it, is then continued medially as the upper margin of the primary foramen magnum. In the calf at the 19-mm. stage (Pls. 12, 13) and at the 40-mm. stage (Pl. 14) the various phases in the formation of the tectum synoticum from the enlarging supraoccipital cartilages of the two sides can be followed out in their entirety. Whether this plan is followed in other mammals remains to be shown. The term tectum synoticum is not altogether a happy one, and had better be abandoned for the term *tectum cranii posterius* (Pl. 8). Its connection with the auditory capsule is indirect, *i.e.* through the parietal plate, and it is also clearly a secondary one. In man there are two tecta (Bolk, Fawcett): one a very wide one, the more posterior, therefore called the *tectum cranii posterius*, from the middle of whose anterior border a processus ascendens arises (Fawcett; in pig, Mead); the other, the *tectum cranii anterius*, is very slender and quite isolated, not reaching the parietal plate on either side, nor being in any way connected with the tectum cranii posterius. Recently, I have observed two tecta in the cat: one certainly the ordinary tectum posterius, the other small, median, and anterior to this, which may be an isolated processus ascendens or may be looked upon as a tectum anterius. It seems to be quite clear that this region of the chondrocranium is in a progressive condition, as Gaupp has stated. In Dasyurus viverrinus (Pl. 15) 9·5-mm.

stage two bars run across the middle line, but both appear to be parts of the tectum posterius, or has the anterior one reappeared in isolated form as in man and cat? This is scarcely probable.

4. The Lateral Commissures.

These are, from before backwards, first the *spheno-ethmoidal* (Pls. 1, 3) (of large size), which connects the anterior basal angle of the ala orbitalis with a backward projection from the frontal prominence of the pars intermedia of the lateral wall of the nasal capsule. Next follows the *orbito-parietal commissure* (Pls. 1, 3), connecting the posterior basal angle of the ala orbitalis with the antero-superior angle of the parietal plate. Finally we may describe the union of the anterior angle or process of the supraoccipital cartilage with the postero-superior angle of the parietal plate as the *occipito-parietal commissure* (Pl. 3); or of course the tectum posterius, stretching as it does from parietal plate of one side to that of the other, may be looked upon as the commissura posterior.

5. The Nasal Capsule (Pls. 1, 2, 3, 4, 5, 6).

This is an enormous structure. Its antero-posterior length amounted in the model to 200 mm., whereas the total length of the central stem behind was only 125 mm.

It consists of a central part, the septum nasi, and two lateral appendages (as Fischer says, it may be compared with a double-barrelled gun). When the whole is viewed from above (Pl. 1) it has a very characteristic pear-shape, of which the larger end or bulb is placed backwards. The whole capsule is more complete than usual, recalling that of the mole (Pl. 9), but it is relatively not so long. The main openings into it are the large subcerebral vacuity on each side of the septum which, at this stage, has not been bridged over by a *lamina cribrosa*; the *fenestra* (incisura) *narina* (Pls. 2, 3, 4) which is placed rather laterally than apically; and the long *fenestra basalis* (Pl. 2) which is seen below. A small *fenestra dorsalis* (Pl. 1) is present just behind the apex of the anterior part of the nasal capsule, recalling somewhat that seen in the mole (Pl. 9), but it is more apically placed than in the latter. No foramen epiphaniale could be found after a most careful search, but a small *cribro-ethmoidal canal* is present.

The *nasal septum* (Pl. 5) is that segment of the pars interorbito-nasalis which is included in the nasal capsule. It is of great length; is partly subcerebral—say one-third; the remainder is precerebral. The subcerebral part is very narrow from above downwards; posteriorly it is also narrow

from side to side (fig. 10); thicker below, however, than above. When traced in the forward direction it rapidly increases in height, its upper border rising in height whilst the lower remains more or less constantly at the same level. The greatest height is reached at the junction of the subcerebral and precerebral parts of the upper border. At the hindmost part of the subcerebral segment of the upper border a cartilaginous bar is given off on each side to connect the septum with the lateral wall of the nasal capsule. This bar I think well to name the *tectum nasi posterius* (Pls. 1, 5). Fischer

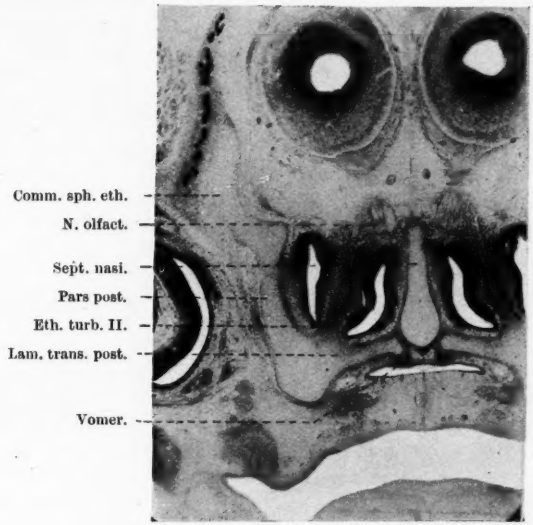


FIG. 10.—*Erinaceus europæus.*

has named the corresponding bar in Talpa the *planum antorbitale*. That term I think better to use in another sense and for another region. At the junctional region of the upper border of the subcerebral part of the septum with the precerebral part two prominences arise on each side. Perhaps they represent a cartilaginous *crista galli*. The precerebral part of the upper border of the septum nasi is attached laterally in its whole length to the tectum anterius (Pl. 1; fig. 11), and as each half of this tectum in passing laterally from the septum arches first in an upward direction, it follows that the precerebral part of the upper border of the septum lies at the bottom of a longitudinal median sulcus, *sulcus dorsalis nasi* (Pls. 1–5). From behind forwards this part of the upper border for

two-thirds of its extent slopes downwards and forwards, forming roughly an angle open below of about 135° with the subcerebral part of the border (Pl. 5). But beyond this point the anterior third runs more horizontally forwards. This part at its anterior end turns suddenly down at right angles to form the anterior border of the septum, and from its lateral margin the wing-like expansions pass in an arched manner forwards, then outwards, and finally backwards to form the *cupula anterior* (Pls. 2, 3, 4, 5) or median alar cartilage on each side, from which there projects the free lateral edge and about its middle a peg-like process, the *processus cupularis* or *processus alaris medius*. The inferior border (Pls. 2, 3, 4, 5) is of great length, and is thicker than either the superior or the anterior border,

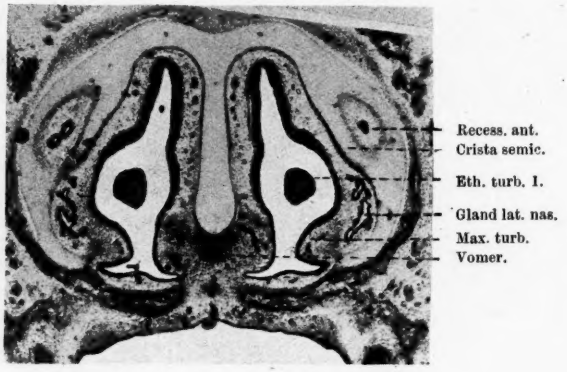


FIG. 11.—*Erinaceus europæus.*

especially in its hinder two-thirds. For about its hinder two-thirds it is comparatively straight and continues almost uniformly the plane of the under aspect of the central stem behind it, being bent at its commencement only slightly at an angle with the latter; but as one reaches the anterior extremity of its hinder two-thirds it rises upwards somewhat and becomes greatly thickened (Pl. 5); then bending downwards at right angles to its original course it joins the anterior third of the lower border, which is much thinner and appears to bifurcate to form more posteriorly the laminæ transversales anteriores, and more anteriorly two triangular plates which are almost a replica of those found in the mole. Perhaps they may be called *processus laterales ventrales* (Pl. 2). The apex of each is separated by a narrow fissure, continuous with the lower segment of the fenestra narina, from the *processus alaris superior v. lateralis* (Pl. 2). From what

has been said, the whole septum viewed from the side has a somewhat triangular form, of which the base is formed by the lower border.

The whole septum is comparatively thin save at its lower border, and in the neighbourhood of the junction of the posterior two-thirds with the anterior third it greatly thickens, and in coronal section has a somewhat pear-shaped form (fig. 12), the larger end of the pear being downwards.

The septum at its lower border (Pls. 2, 5) has numerous important relations. Commencing behind, there are at each side of this border the following structures: first, the *lamina transversalis posterior*, separated by a narrow fissure from the septum (fig. 10); next, the corresponding lamella of the *vomer*, which stretches from the lamina transversalis posterior as

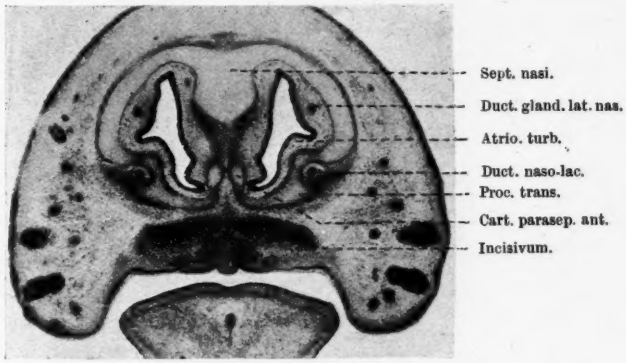


FIG. 12.—*Erinaceus europæus.*

far as the medial side of the hinder end of the organ of Jacobson; next, the free part of the organ of Jacobson; next, the medial lamella of the *anterior paraseptal cartilage* (fig. 13); then a thick band of connective tissue (fig. 12), which stretches between the thick part of the lower border of the septum and the narrow cylindrical stalk of the medial lamella of the paraseptal cartilage and the median part of the hinder edge of the lamina transversalis anterior; next, the *lamina transversalis anterior*, which is directly continuous with the septum; finally, the base of the *processus lateralis ventralis* (fig. 14).

The *lateral part of the nasal capsule* (Pls. 6, 3, 4) may be described as consisting of the following parts: a roof, composed of a small tectum posterius; a large tectum anterius; a lateral wall (paries nasi); a floor; an anterior wall (cupula anterior); and a posterior wall (cupula posterior).

The roof (Pls. 1, 5, 6) is partly subcerebral and partly (mainly) pre-

cerebral. The subcerebral part of the roof is complete posteriorly, forming the *tectum nasi posterius*,—a bar of cartilage, quite flat as seen from the cavum cranii (Pl. 1), which stretches outwards from the upper border of the subcerebral part of the septum to the lateral wall. The remainder of the subcerebral part of the roof, represented in older stages by the lamina cribrosa, is wanting at this stage. The precerebral part of the tectum is complete save near the apex, where it is perforated by the small *fenestra dorsalis* (Pls. 1, 5), which in the recent condition is filled with fibrous tissue and a blood-vessel. In its whole length this part of the tectum

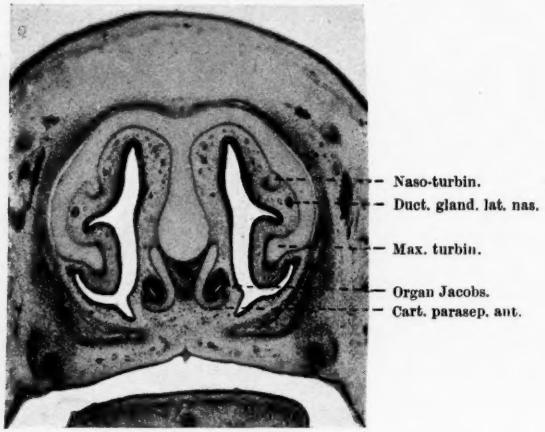


FIG. 13.—*Erinaceus europæus.*

(tectum anterius) is slightly convex from side to side, the two convexities producing the median dorsal sulcus, at the bottom of which the upper margin of the precerebral part of the septum lies. Almost insensibly the tectum passes into the lateral wall or *paries nasi* (figs. 11, 12, 13, 14).

The lateral wall, as seen from the exterior (Pls. 3, 4), shows the three divisions already mentioned in connection with roof, viz. the *pars posterior pars intermedia*, and *pars anterior*. These parts are separated from one another by curved sulci, thus—the pars posterior is separated from the pars intermedia by the *sulcus lateralis posterior*. This is a curved sulcus, convex forwards, which stretches from the upper margin of the lateral wall of the nasal capsule behind the attachment of the spheno-ethmoidal commissure forwards, then downwards, and finally somewhat backwards to reach the lower margin of the lateral wall. It is not very well marked,

especially below, but it coincides in the interior with the main attachment of the first primary ethmo-turbinal. The *sulcus lateralis anterior* is likewise not very well marked, but it may be traced in a downward and forward direction from the cribro-ethmoidal foramen to the lower edge of the lateral wall.

Of the three divisions of the lateral nasal capsule, the pars anterior is in length almost the equal of the pars intermedia and pars posterior taken together.

The *pars posterior* commences behind at the cupula posterior, and is triangular in shape, the apex being at the said cupula and the base at the sulcus lateralis posterior. Its upper margin is subcerebral, and here forms

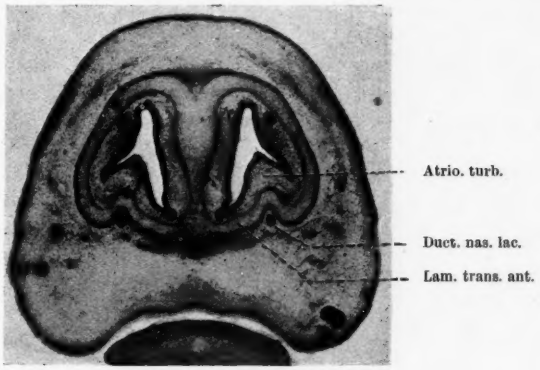


FIG. 13A.—*Erinaceus europæus.*

the outer wall of the olfactory vacuity. Its lower margin is sharply defined, and when traced inwards is seen to be continuous with the outer edge of the lamina transversalis posterior. This margin in the complete condition is in relation with the os palatinum. The lateral surface of the pars posterior is flattened or even slightly hollowed out, and, being in relation to the orbit, is called *planum antorbitale*; but the planum antorbitale extends beyond this region on to the posterior aspect of the pars intermedia, and it obscures the postero-lateral sulcus somewhat by doing so.

The *pars intermedia* is placed between the antero-lateral and postero-lateral sulci, and possesses the greatest height of the three parts into which the lateral wall is divided. It shows three prominences, viz. a *prominentia superior* or *frontalis*, a *prominentia inferior* or *maxillaris*, and between

the two in front a *prominentia anterior*. This last is ill marked. Each of these prominences is caused by a corresponding hollow on the internal aspect. To the prominentia superior or frontalis the spheno-ethmoidal commissure is attached, while from the front of the prominentia inferior v. maxillaris the inferior oblique muscle of the eyeball arises.

The sulcus lateralis anterior, which delimits the pars intermedia anteriorly, corresponds in the interior with the greater part of that important landmark the *crista semicircularis* (Pl. 6).

The lower half of the anterior surface (Pl. 4) of the maxillary prominence is covered by the maxilla, and at this stage the hinder part of the frontal prominence is covered by the frontal bone; and as these bones, so far

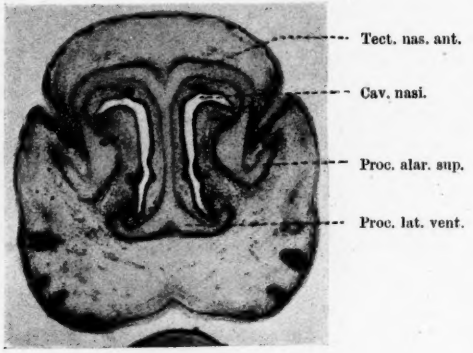


FIG. 14.—*Erinaceus europæus.*

as I know, always have this relation to the prominences in question, I have given the alternative names to them.

The inferior margin of the pars intermedia is slightly inrolled, and forms in its anterior part a portion of the maxillo-turbinal (Pl. 6; fig. 13), which, however, chiefly belongs to the pars anterior.

The *pars anterior* (Pls. 3, 4) is of considerable length, as has already been stated; but it is of only moderate height, a height which is pretty uniform throughout. Superiorly, it runs into the tectum anterius at a rounded superior border; posteriorly, it is separated from the pars intermedia by the antero-lateral sulcus. The inferior border can be divided into three parts; the hinder part, equal in length to the other two combined, is inwardly projected as a shelf, and along its greatest convexity runs the naso-lacrimal duct. Here too the mucous membrane

of the nasal sac projects sufficiently low down to be visible from the lateral aspect, but that is not shown in the model. There is no lamina infraconchalis such as occurs in the rabbit (Voit) or in the model of Microtus, from which the mucous membrane has been removed (Fawcett).

One may see at some depth the greater part of the anterior paraseptal cartilage as well as the organ of Jacobson, which rests in its concavity (Pl. 3). The anterior end of this part of the inferior border ends at the lamina transversalis anterior; the next stage of the inferior border is fused with the outer edge of that lamina; a deep gutter, in which the naso-lacrimal duct is lodged, marks the line of junction of lamina with the inferior border (fig. 12). In front of the lamina the final part of the inferior border becomes free, forming the lateral margin of a small notch, the incisura pretransversalis, through which the naso-lacrimal duct passes to fuse with the mucous membrane of the nasal sac.

The anterior border of the pars anterior forms the hinder margin of the fenestra narina, which in Erinaceus is directly laterally; it is incurved about its middle, forming a somewhat triangular plate which is the anterior end of the *atrio-turbinal* (Pl. 2).

The *fenestra narina* (Pls. 2, 3, 4) is a somewhat dumbbell-shaped vacuity directed laterally. Its anterior border is formed by the cupula anterior, from whose middle there projects laterally and in a somewhat downward direction a cupular spine. Its posterior border is formed by the anterior margin of the pars anterior, and, as the cupular spine and the anterior end of the atrio-turbinal project towards one another somewhat opposite the middle of the fenestra, it is constricted into an upper and a lower large segment. The fenestra is bounded below by the processus alaris superior, a triangular piece of cartilage which is somewhat bent, so as to be convex externally. Behind this plate of cartilage the naso-lacrimal duct reaches the nasal sac.

The floor (solum nasi) (Pl. 2) of the nasal capsule is incomplete, more so than it is in the rabbit or Dasyurus or Microtus. There is a large vacuity in it, the *fenestra basalis*; moreover, a narrow fissure, representing the *septo-paraseptal fissure* of other mammals, intervenes between the anterior paraseptal cartilage and the septum, and between the median edge of the lamina transversalis posterior and the septum. The fenestra basalis is even relatively larger in Erinaceus than it is in the above-mentioned forms, because the paraseptal cartilage is incomplete: all that narrow cylindrical part such as is seen in the animals before cited being absent. The structures entering into the *solum nasi* are the following: behind, the *lamina transversalis posterior*; in front, the *lamina transversalis anterior*, from whose inner end is projected backwards half way

along the medial aspect of the fenestra basalis the bilaminar *anterior paraseptal cartilage*. These parts may be examined seriatim:—

The *lamina transversalis posterior* is a triangular plate whose apex is at the cupula posterior, whose base is free, forming the posterior boundary of the fenestra basalis, and whose median end lies along the infero-lateral margin of the septum nasi, separated from it wholly by a narrow fissure—the posterior moiety of the septo-paraseptal fissure (fig. 10). The median edge of the lamina near the cupula is covered by the perpendicular plate of the os palatinum, whilst anteriorly the same edge is covered by and is perhaps being commandeered by the ossifying corresponding lamella of the vomer. The outer side of the lamina is fused with the inferior margin of the pars posterior of the lateral wall, and when viewed from above it can be seen that the second primary ethmoid-turbinal springs from the site of fusion of the two. (I have used the term "fusion" here to express continuity of the two structures, not to infer that they were ever separate.) The region to which the lamina transversalis posterior belongs is one of very great interest, and it has been discussed at considerable length by Eugen Fischer in his description of the skull of Talpa. It cannot be said that anything like settlement has been reached regarding its fate, but what is certain is that the cupula posterior extends backwards, being pushed backwards by the backward growth of the nasal mucous sac. It finally becomes jammed against the point of the apex of the ala orbitalis [(?) ala hypochiasmata], and takes a part in the formation of the cartilaginous body of the sphenoid; and so much is the median part of the body—*i.e.* the part derived from the hinder end of the pars interorbito-nasalis (presphenoid)—compressed between the cupulæ of the two sides that it is reduced to a very narrow septum when ossified, which projects in the middle line as the rostrum of the sphenoid and in front as the ethmoidal crest. By what mode exactly the cupula is replaced by bone is not as yet certain, but a glance at the fully-formed sphenoidal turbinal at a time before that has become fused to the rest of the body of the sphenoid gives a facsimile of the cupula as seen from below. Whether, then, the sphenoidal turbinal ossifies from the cartilaginous cupula or from its perichondrium or from the fibrous remnant of the former, and whether by one centre or by many, as Cleland has described, remains uncertain.

The Lamina transversalis anterior (Pl. 2).—This is of large size and quadrilateral in form; moreover, it is convex downwards and about a horizontal plane. Medially, it is to a large extent in direct continuity with the lower margin of the septum nasi; but as this border is traced backwards it becomes free of the septum, and from its hinder edge a narrow rod

of cartilage runs backward to connect it with the anterior paraseptal cartilage, to which we will return later. The lateral border is directly continuous with the under edge of the anterior part of the lower border of the pars anterior of the lateral wall of the nasal capsule, and at the line of junction a deep groove—the *naso-lacrimal* sulcus—lodges the naso-lacrimal duct (fig. 12). The anterior border is V-shaped and free; the apex of the V is the incisura pretransversalis, through which the naso-lacrimal duct reaches the nasal mucous sac. The posterior border of the lamina transversalis anterior is free, and forms the anterior boundary of the fenestra basalis. From its medial end, at its junction with the medial border of the lamina, the narrow cartilaginous stalk of the anterior paraseptal cartilage is given off, whereas from its lateral edge an extraordinary cartilage passes outwards almost horizontally, but with a slight curve (whose concavity is upwards) (fig. 12), as far as the outer contour line of the pars anterior of the lateral wall of the nasal capsule. This bar of cartilage I have not met with in any other animal. Between it and the junctional region of the outer edge of the lamina transversalis anterior and the lower edge of the lateral wall of the pars anterior of the nasal capsule, the naso-lacrimal duct enters the naso-lacrimal sulcus from behind, so that the root of this bar conceals the duct from view as seen from below. The bar itself is covered below by the body of the os incisivum. From its direction the bar may be called the *processus transversalis* (Pl. 2).

The Anterior Paraseptal Cartilage (Pl. 2).—This cartilage commences in a narrow stalk which runs back from the angle of junction of the medial with the posterior border of the lamina transversalis anterior. This stalk is placed at some depth from the general inferior plane of the lamina and main mass of paraseptal cartilage, so that the appearance is that of a deep notch in the paraseptal cartilage. This notch is occupied by the connecting stalk of bone between the main mass of the os incisivum and its "paraseptal" process. The main part of the anterior paraseptal cartilage between this notch and stalk is bilaminar, consisting of a large medial lamella which is outcurved below to form a gutter in which rests the organ of Jacobson (fig. 13). The medial lamellæ of the opposite paraseptal cartilages are very closely approximated by their medial surfaces, only a certain amount of connective tissue and the "paraseptal" processes of the ossa incisiva intervening in the anterior half of the inter-paraseptal space (Pl. 2; fig. 13). Each medial lamella is suspended from the side of the lower part of the nasal septum by dense cellular tissue. The anterior end of the bilaminar part projects downwards and forwards and lodges the duct of the organ of Jacobson. This duct, distinguished from the organ itself by the different character of the epithelium lining it, ends ultimately

at the inner side of the middle of the naso-palatine duct. The body of the organ projects backwards beyond the hindmost limit of the paraseptal cartilage for a short distance (Pl. 5), and it is in the space between the two "organs" that the anterior ends of the vomer appear (Pl. 2).

The Medial Aspect of the Lateral Wall of the Nasal Capsule (Pl. 6).—This, like the lateral aspect, may be divided into three parts, and these parts are much more readily distinguished from one another from this aspect. The parts are as before: a pars anterior, a pars intermedia, and a pars posterior. The pars anterior is only imperfectly separated from the pars intermedia by a crest, the *crista semicircularis*, which stretches from above in the region of the cribro-ethmoidal foramen, which has perforated it, in a downward and forward direction for half the depth of the lateral wall of the capsule; the crest then becomes very low, running downwards and backwards to end in the lateral wall of the maxillary recess. This lower part of the crista semicircularis may be looked upon as the representative of the processus uncinatus, when that exists, of the later ethmoid.

The pars intermedia is the deepest segment of the lateral wall. It is bounded behind by the first primary ethmo-turbinal, and reaches back to the cupula nasi posterior.

Considering these parts now in detail, and commencing with the pars anterior, it may be said at once that it is by far the longest segment. It is roughly quadrilateral in outline, deepest behind, narrowing about its middle to again deepen somewhat in front. Its upper border stretches from the upper end of the crista semicircularis as far as the upper edge of the fenestra narina, and is slightly concave on its upper aspect. It is thickest behind. Its lower border or boundary is formed of several parts: in front, by the processus alaris inferior; behind, that of the lamina transversalis anterior, which is here upcurved to form a large part of the *atrio-turbinal*; behind the lamina transversalis anterior the lower border is formed by the maxillo-turbinal for a considerable distance—in fact, in almost the remainder of its extent; its final part posteriorly is formed by the lower edge of the *recessus glandularis*, of which more will be said later. The anterior boundary is short, and its middle is swung medially in the form of a triangular plate which forms the commencement of the atrio-turbinal. The posterior boundary or border is only well marked in its upper half, where it is formed by the crista terminalis.

The general *medial surface* of the pars anterior is markedly concave from above downwards, but from end to end shows about its middle a slight convexity.

This region shows us three turbinal cartilages, which are the *atrio-*

turbinal, the *maxillo-turbinal*, and the *naso-turbinal*. The *atrio-turbinal* (Pl. 6) commences anteriorly as a triangular inrolling of the middle of the posterior wall of the fenestra narina. At the middle of its base a small vacuity is seen; the lower basal angle of the triangular plate is continuous with the ridge on the upper aspect of the lamina transversalis anterior caused by the sulcus naso-lacrimalis above described, so this ridge is a part of the atrio-turbinal. Posteriorly the atrio-turbinal is directly continued into the maxillo-turbinal without any notch of separation such as exists in the rabbit (Voit) and the water-rat (Fawcett). The *maxillo-turbinal* (Pl. 6) is the medially-rolled lower edge of the pars anterior behind the plane of the lamina transversalis anterior. It may in this case be regarded as the direct backward continuation of the atrio-turbinal. It does not quite correspond with the whole of the lower free border of the pars anterior, which lies posterior to the lamina transversalis anterior. If that border be traced backwards with the microscope, section by section, it will be found that the mucous membrane which covers it, and which forms the actual conchal projection into the nasal cavity, gradually dies away and ceases to project at a spot perpendicularly below the lower end of the crista terminalis. The *naso-turbinal* (Pl. 6; fig. 13) is of small size, and may be traced forwards from the front of the lower end of the crista semicircularis about midway between the upper and lower borders of the medial surface of the lateral wall of the nasal capsule. Unlike that of the rabbit and of the water-rat, it is attached by its whole length to the lateral wall, and at this stage reaches from the crista semicircularis only one-third of the way towards the anterior margin of the lateral wall (Pl. 6). It partially divides the cavity of the nose into an upper and a lower channel. The lower channel has been named in the rabbit the *sulcus supraconchalis* (Voit). It lodges here a considerable part of the lateral nasal gland.

The *pars intermedia* (Pl. 6) is entered by a crescentic somewhat wide fissure. Anteriorly it is imperfectly cut off from the pars anterior by the crista semicircularis, but below that crest it is continuous with the pars anterior through the recessus glandularis. Posteriorly it is limited by the first primary ethmo-turbinal, which overhangs its medial side to a very considerable extent and so reduces the entrance into the general nasal cavity to a crescentic fissure. Below, the pars intermedia is bounded by the junction of the first ethmo-turbinal with the lower border of the lateral nasal wall; whilst above, the pars intermedia opens into the cavum cranii through the large olfactory vacuity.

The general concavity of the pars intermedia is divisible into a series of recesses, of which the main ones are the recessus superior v. frontalis and the recessus inferior v. maxillaris. These recesses are imperfectly

separated from one another by the anterior root of the first ethmo-turbinal. In front of this root they communicate with one another and form the point of communication; a small but somewhat deep recess, the *recessus anterior*, projects forwards under cover and therefore to the lateral aspect of the lower half of the crista semicircularis proper. A fourth recess, but very shallow, is found at the antero-inferior part of the recessus maxillaris; this recess, the *recessus glandularis* (fig. 11), is continuous posteriorly with the recessus maxillaris and anteriorly with the sulcus supraconchalis of the pars anterior. These various recesses produce corresponding elevations on the exterior of the pars intermedia, but these are not very readily distinguished on that surface, either because the model is not so well made as it might be or because the corresponding prominences are not well marked.

The *recessus frontalis v. superior* (Pl. 6) is of large size; freely communicating above with the cavum cranii, overlapped medially by the upper half of the first primary ethmo-turbinal, and below partly shut off from the recessus maxillaris v. inferior by the anterior root of the turbinal just mentioned, it communicates anteriorly with the recessus anterior, and below, in front of the anterior root of the first primary ethmo-turbinal, with the recessus inferior. Its outer wall is marked by one low frontal turbinal which divides it imperfectly into an upper and a lower channel. A special bundle of olfactory nerves arises from the mucous membrane lining the frontal recess and enters the olfactory bulb. The *recessus maxillaris* is a large and deep recess lying under cover of the lower part of the first ethmo-turbinal and below its anterior root; it is crossed in front of its middle by a low-curved ridge in continuity above with the crista semicircularis and on the outer wall of the recess. This ridge, which I have before mentioned as being probably homologous with the root part at all events of a processus uncinatus, cuts off from the recessus maxillaris a part in front and below in which is lodged the lateral nasal gland (fig. 11); and the actual fossa in which the gland lies is the fourth recess of the pars intermedia, viz. the *recessus glandularis*. This recess, as has been before mentioned, is directly continued into the sulcus supraconchalis.

The *pars posterior* v. ethmo-turbinalis is characterised by the presence in it of well-marked ethmo-turbinals. These in Erinaceus are two in number at the stage modelled. In general outline it is quadrangular in form, having therefore four borders, which are a superior, an inferior, an antero-superior, and an antero-inferior. The superior and inferior borders meet at an acute angle posteriorly—at, in fact, the cupula posterior. The superior border is in great part free, and forms the posterior boundary of the orbito-nasal fissure. At its inner end it is, in its upper three-fourths, fused with

the nasal septum and only artificially displayed by section. The lower part is free and directed towards the septum nasi—separated from it, however, by the posterior moiety of what has been previously called the septo-paraseptal fissure. The inferior border in its anterior half is formed by the lower edge of the lateral wall of the pars posterior, in its posterior half by the inner edge of the lamina transversalis posterior. The antero-superior border is formed by the upper half of the free edge of the first primary ethmo-turbinal, the antero-inferior border by the lower half of the free edge of the same turbinal. Two turbinals are found in connection with this region which from before backwards are the first and second primary ethmo-turbinals (I use the term primary in the sense of priority of development). At this stage there are no secondary ethmo-turbinals. By means of the second primary ethmo-turbinal the general cavity of the pars posterior is divided into two meatūs, viz. a superior or posterior behind the second primary ethmo-turbinal and an inferior or anterior in front of it.

The primary ethmo-turbinals (Pl. 6), as has been said, are two in number, viz. first and second. The first primary ethmo-turbinal is of large size, and extends between the upper and lower borders of the pars posterior. It is attached to the lateral wall by three roots, viz. an upper, lower, and an anterior, all of which, with the exception of the anterior, are continuously attached to the outer wall. The anterior root is bridge-like, being attached only at its anterior and posterior extremities. It runs forwards into the pars intermedia and incompletely separates it into the recessus frontalis and the recessus maxillaris. The upper and lower roots are much in the same continuous line, attached to the lateral wall, a line of attachment which is indicated on the exterior by the sulcus lateralis posterior. From these roots of equal length the main plate is formed which stretches from upper to lower borders of the pars posterior; the medial surface of the plate so arising forms a large part of the lateral wall of the pars posterior, and the free edge of the plate, which looks forwards as well as a little medialwards, forms the most anterior limit of the pars posterior. This free edge really consists of about three equal parts, joined at two angles, of which the lower is the more prominent. The upper part of the free edge is almost horizontal and directed inwards and forwards. The next part bends downwards and forwards to the angular projection above mentioned, whilst the lower part of the free edge runs downwards and somewhat backwards to the lower edge of the lateral wall of the nasal capsule. It is the angle of junction of the middle and lower parts of the free border which constricts the opening into the pars intermedia. The medial surface of the first primary ethmo-turbinal is marked by a faint ridge which runs downwards and forwards and is a hint at a subsequent

bilamellar condition of this turbinal, such as frequently exists in other animals. It would seem from the specimens at my disposal that that unilamellar condition is the primary one ontogenetically and phylogenetically.

The second primary ethmo-turbinal is almost a replica in small form of the first, but it has no anterior root, and it shows no sign of being bilamellar. Its root stretches from the upper free border of the pars posterior to the junction of the lamina transversalis posterior with the lower edge of the lateral wall of that region (Pl. 6; fig. 10). Its anterior free edge repeats in smaller form that of the anterior edge of the first primary ethmo-turbinal. By it the cavity of the pars posterior is divided into two meatūs, and it develops later than the first ethmo-turbinal. It is likely that it owes much of its development to the backward growth of the nasal sac. Whether more than two primary ethmo-turbinals are developed in Erinaceus, I know not.

The position of the ethmo-turbinals, especially the first, and of the crista semicircularis strongly suggest that these structures play an important part in the modelling of the nasal capsule, and that they, by acting as strengthening rods, as it were, or internal buttresses to this wall, prevent its being outpouched at their sites of attachment; hence, as the nasal sac grows it tends to cause the lateral wall of the capsule to bulge outwards at three spots, viz. in front of the crista terminalis, between it and the first ethmo-turbinal, and behind the first ethmo-turbinal. In this way the various divisions of the exterior are brought about.

Morphology of the Parts of the Solum Nasi.—Some remarks may be made regarding the morphological history of certain structures forming the solum nasi, more especially of the lamina transversalis anterior, the paraseptal cartilages, and the lamina transversalis posterior. In the majority of mammals below man, perhaps in all, the lamina transversalis is present, and in the majority it connects the septum with the lateral wall, a true zona annularis being formed; but in Lepus this lamina is stated by Voit—and I confirm his statement—to be separated from the septum by a narrow fissure.

The posterior paraseptal cartilage seems to be present in some form or other in all mammals hitherto examined. Its presence is usually denied in man, but in a model made by me of the nasal capsule of a 65-mm. embryo, it is certainly present, though small. It is formed by the hollowing out of the planum antorbitale due to the backward growth of the nasal sac, and the floor of the hollow is the lamina. Its form is usually triangular, with base forwards and straight; but if concave, its inner basal angle projects forwards as the posterior paraseptal cartilage. The anterior paraseptal cartilage in the lower mammals commences anteriorly at the inner part of

the hinder border of the lamina transversalis anterior by a transversely or vertically deep root, depending upon the animal; it grows backwards by the side of the lower part of the septum and ends posteriorly in a sharp point close to the inner end of the posterior wall of the nasal capsule. When that wall comes to be hollowed out and thrust back by the backward growth of the nasal sac, the lamina transversalis posterior is formed as the floor of the hollow and the posterior end of the anterior paraseptal cartilage fuses with its inner basal angle; by the still greater thrusting back of the posterior wall of the capsule, and perhaps too by intrinsic growth, this junctional region is drawn out into a slender cylindrical rod. Such is the mode of development in Dasyurus; it is similar in Lepus, and in all where there is a complete common paraseptal cartilage. Now this common paraseptal cartilage has on its medial side the corresponding lamella of the vomer, and the vomer tends to invade and surround the narrow cylindrical part and, as we rise in the scale of mammals, to replace it altogether. That condition is well seen in the cat, and in such a condition the vomer makes use of the perichondrial connecting link between the posterior and anterior paraseptal cartilages—in other words, ossifies at its expense. This is very well seen in the ferret and in man. Meanwhile certain changes are taking place in regard to the anterior paraseptal cartilage. As already said, that cartilage arises by an either transversely wide or vertically deep root from the anterior paraseptal cartilage. In Dasyurus it is wide transversely, in the ruminant it is deep. But in Erinaceus and Talpa the commencement of this cartilage is quite narrow; it looks in fact, as seen from the side, as if there were a large notch in it below. This notch is occupied by the commencement of the paraseptal process of the premaxilla, which process is continued backwards along the median side of the anterior paraseptal cartilage, which behind the premaxillary notch has become bilaminar. When we examine the anterior paraseptal cartilage in the ferret and in the cat, we find that the narrow connecting piece above the paraseptal process of the premaxilla is absent, and the bilaminar part is left stranded by the side of the lower border of the septum, in direct continuity with neither lamina transversalis anterior nor with the posterior paraseptal cartilage (if that exists). Its isolation has in each case been brought about by the presence of bone. It still retains the bilaminar form, and the organ of Jacobson rests in the hollow between these laminæ. When we reach man, not only has the anterior paraseptal cartilage become isolated as in the cat or ferret, but it has lost its lateral lamella, and it no longer retains any relation to the organ of Jacobson, for that lies stranded high up on the septum nasi. So complete is the separation between paraseptal cartilage and organ that Michalkovics supposed that the organ

is not really the organ of Jacobson, but the duct of a septal nasal gland. There can, however, be little doubt that this structure is the organ of Jacobson.

In man a still greater change has taken place in the cartilage of the solum nasi, for the lamina transversalis anterior has disappeared, so that in him the fenestra narina and the fenestra basalis have run together to form one large vacuity, the *rostro-ventral fissure* of Gaupp.

The Visceral Skeleton (Pl. 3).

This consists of, from above downwards, the mandibular arcade, next the hyoid arch, then the first, second, and third branchial arch cartilages.

The mandibular arcade consists, from behind forwards, of the incus cartilage, the malleus cartilage, and Meckel's cartilage, the two latter being in direct histological continuity with one another. The incus cartilage is of the usual form, with a short posterior process lying in a fossa incudis above and medial to the crista parotica, and a long processus which descends somewhat medially and articulates through the medium of a well-marked meniscus of connective tissue with the head of the stapes cartilage. The front of the body of the incus articulates in the usual way with the head of the malleus cartilage.

The malleus cartilage is massive, and sends downwards and then suddenly medialwards a strong *manubrium*; from the front of the malleus cartilage Meckel's cartilage passes forwards with a slight bend downwards and finally upwards in a generally convergent direction towards its fellow of the opposite side. It preserves in an unusual degree a cylindrical form in the greater part of its forward course. It soon comes to lie against the medial side of the bony mandible—at, in fact, the root of the processus coronoideus,—and it continues its course onwards on the medial side of the body of the mandible, becoming somewhat flattened from side to side as it nears the anterior extremity of that bone; then, about the spot where the bone comes to an end, the cartilage fuses with its fellow of the opposite side, and the two fused cartilages project forwards for some distance beyond the bone in a somewhat conical spinous process. Nowhere at this stage is the cartilage enclosed by bone, nor does it show any sign of ossification at this stage.

The *hyoid cartilage*. This consists of two parts: a long hinder part fused directly to the lower edge of the crista parotica and passing forwards from thence with a somewhat sinuous course; having nearly reached the anterior extremity of the thyro-hyal, it suddenly ends, to be succeeded by an ovoidal cartilage which is clearly the *cerato-hyal*. The stapes, which

developmentally belongs to this arcade, is at this stage freed from any connection with it, and is only remarkable in being perforated by a very large stapedial artery.

The *thyroid arcade* consists of a large thyro-hyal which posteriorly is directly continuous with the upper hinder angle of the thyroid cartilage; anteriorly it articulates with both the cerato-hyal and the body of the hyoid (Parker's basi-branchial).

The *thyroid cartilage*, or cartilage of the second branchial arch, is of large size, and consists of two small alæ fused near the lower part of their medial borders. The postero-superior angle of each ala is directly continuous with the hind end of the thyro-hyal, whilst the postero-inferior angle articulates by a well-marked inferior cornu with the side of the cricoid cartilage. Each ala is perforated by two large foramina, which lie in the same vertical line.

The cartilage of the fifth arch, viz. the *cricoid cartilage*, is of the usual form of completed cricoid, and articulates in the usual way with the thyroid cartilage and the two arytenoids.

The large size of the thyroid cartilage is in striking contrast to that in the mole, in which the ala of the thyroid is in the form of a cylindrical rod, from which, if Symington be correct, one may conclude that the vocal powers of Erinaceus are much more highly developed than those of Talpa.

The Osseous Skeleton (Pls. 1, 2, 3, 4).

The following bones are now ossified: the parietals, frontals, nasals, premaxillæ, maxillæ, palatines, vomer, squamosals, and mandible.

The *os parietale* (Pl. 3) is of comparatively large size, covers the upper half of the parietal plate of cartilage, the whole length of the orbito-parietal commissure and a part of the ala-orbitalis as far down as the sulcus for the onward continuation of the supraorbital artery.

The *os frontale* (Pl. 3) is comparatively small, overlaps the ala orbitalis as far down as the same sulcus, and then passes forwards along the outer surface of the spheno-ethmoidal commissure as far as the frontal prominence of the pars intermedia of the lateral wall of the nasal capsule, which it covers only to a slight extent posteriorly.

The os nasale (Pls. 1, 3) is very small at this stage, and lies upon the hinder part of the tectum of the pars anterior of the nasal capsule.

The os incisivum (premaxilla) (Pls. 1, 2, 3, 4) is well formed, and consists of a body which underlies the processus transversus of the lamina transversalis anterior. The body gives upwards and backwards from the hinder and outer part of its upper surface a short process, obviously the com-

mencement of the frontal process of the os incisivum, and a gap separates this from the corresponding process of the maxilla. From the medial end of the body of the premaxilla a long *paraseptal process* (Pl. 2) is given off; this passes at first medially into the notch between the medial lamella of the anterior paraseptal cartilage and the lamina transversalis anterior, no doubt causing that notch, as Fischer observed in Talpa. The paraseptal process now goes directly backwards on the medial aspect of the medial lamella of the anterior paraseptal cartilage, and is so continued for about half the length of that lamella. It is not possible to say whether it ossified independently or not.

The *maxilla* (Pls. 1, 2, 3, 4) is of large size, and consists of a body with frontal, palatine, zygomatic, and outer alveolar processes. Between the outer alveolar and the palatine process tooth-buds are present. The body is perforated by a very large infraorbital foramen (Pl. 4), through which runs the infraorbital nerve. Above the foramen the broad frontal process ascends over the lower part of the maxillary prominence of the pars intermedia of the nasal capsule, and at the same time over the naso-lacrimal duct. The palatine process is of very large size, passes medially and horizontally towards the middle line, forming a floor to the greater part of the fenestra basalis of the solum nasi; from the junction of the palatine process with the body of the maxilla the external alveolar process depends. Between the anterior edge of the palatine process of the maxilla and the posterior edge of the corresponding process or plate of the premaxilla is the primary choana, through whose inner end the naso-palatine duct and the terminal part of the duct of Jacobson's organ project. The zygomatic process of the maxilla is a great length, and passes backwards half-way under the cavity of the orbit to end in a free pointed extremity. To its medial side tooth-buds are found, so that perhaps the term *alveolo-zygomatic process* would be a better one for it.

The *zygomaticum* is only ossified to the very slightest extent, and no attempt has been made to model it. It, however, may be seen with the microscope behind the pointed end of the alveolo-zygomatic process of the maxilla. There seems to be some difficulty about the zygomaticum of insectivora. In some cases it is said to be absent, *e.g.* Centetes; in others very small; but Fischer, in his description of the model of Talpa, says "the jugal is found lateral to the maxilla, passing backwards from the latter as a cylindrical arch (fig. 2). The infraorbital nerve runs over the attachment of this arch. In the full-grown animal it is attached by two limbs to the maxilla; the upper limb here fails. It has not yet reached the squamosal behind, but small masses of bone in the tissues show its future course."

In my own model of Talpa (19 mm.) (Pl. 21) there certainly is a cylindrical rod passing backwards from the body of the maxilla below the infraorbital nerve, and there is no upper limb going from it to the maxilla to complete the infraorbital canal. In my Erinaceus model (25 mm.) this cylindrical rod likewise goes back from the maxilla, and has an upper limb completing the infraorbital foramen. But this I have already described as the alveolo-zygomatic process of the maxilla, for I cannot see that it is separate from the maxilla; nor is it so in Talpa, not even at the 15-mm. stage. Then too its relation to the tooth-buds, I think, proclaims its maxillary nature, since some of the alveoli are formed in part of it. The jugal or malar bone, then, is nearly absent at this stage; what there is of

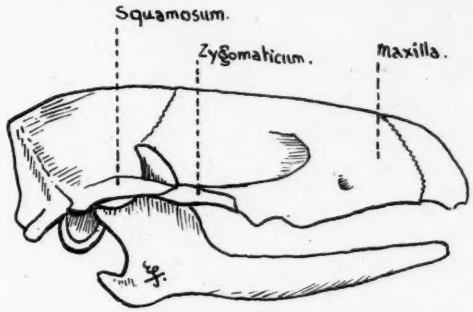


FIG. 15.—*Erinaceus europæus.* Right lateral aspect of adult skull.

it occupies a little, a very little, of the gap between the alveolo-malar zygomatic process of the maxilla and the anterior end of the squamosal.

In the adult Erinaceus (fig. 15) a quite well-marked zygomaticum is present, but it occupies, perhaps, a somewhat peculiar position. What happens is that the alveolo-zygomatic process of the maxilla articulates with the squamosum, and the zygomaticum is placed lateral to that articulation, hiding it from view as looked at from the side. Both alveolo-zygomatic process of maxilla and zygomatic process of squamosum as they approach one another are bevelled at the outer surface, and in the resulting concavity the zygomaticum rests.

The *squamosal* (Pl. 4) is a small bone which commences behind opposite the middle of the outer side of the short process of the incus cartilage; it increases rapidly in height, and perhaps reaches its maximal height opposite the incus-malleus joint. Here its upper margin widens sufficiently to form a surface, over which lie the hinder fibres of the temporal muscle. The bone rapidly diminishes in size as it is traced forwards, and it ultimately

terminates opposite the hinder edge of the processus coronoideus of the mandible. For a considerable part of its length it is separated from the condyle of the mandible by the still cellular discus articularis, above and below which no joint cavity is as yet demonstrable.

The *palatinum* (Pl. 2; fig. 8) is a somewhat curious bone, consisting of a palatine process placed for the most part in front of its vertical plate and only connected with the latter by a narrow stalk, and that to the lower part of its interior edge. The palatine process is imperfectly ossified, and from a common stalk connected with the vertical plate it spreads forwards under the lamina transversalis posterior of the solum nasi towards the palatine process of the maxilla, from which it is, however, separated by a considerable interval. The vertical plate really arches somewhat upwards, forwards, and inwards to reach the infero-lateral aspect of the "central stem," and stretches forwards from the level of the cranio-pharyngeal canal as far as the under aspect of the hinder part of the cupula nasi posterior. It bounds the hinder part of the naso-pharyngeal duct laterally (fig. 8). On its supero-lateral aspect is placed the spheno-palatine ganglion. From its infero-lateral angle the pterygoideus internus arises. The periosteum, in which the upper edge of the vertical plate is embedded, seems to be practically directly continuous with that of the hind end of the vomer.

The *vomer* (Pl. 2) consists here of two long narrow lamellæ, each of which commences behind at the medial edge of the corresponding lamina transversalis posterior, to which it is closely applied (fig. 10). Where the lamina ceases, the vomer is continued forwards infero-lateral to the septum nasi to the interval between the hinder end of the organ of Jacobson and the septum. Here the two separate plates of which the vomer is formed come to lie very close to one another, and it is here that they will first unite. From its position there can be no doubt that the vomer is primarily a covering bone to the medial edge of the solum nasi—in other words, to the common paraseptal cartilage when that exists and to the lamina transversalis posterior. Its relation to the septum as a covering bone—*i.e.* when the two lamellæ have united below the septum—is clearly a secondary one.

The hinder end of each lamellæ reaches very close to the vertical plate of the palate bone behind; the anterior end of the vomer is separated by a considerable interval from the hind end of the paraseptal process of the premaxilla.

The *mandible* (Pls. 3, 4) consists of two separate halves, each closely applied to the lateral aspect of the corresponding Meckel's cartilage. The constituent parts of each half are a body splitting above into outer and inner alveolar walls, a coronoid process, an angle, and a condyle. The common mass from which angle coronoid process and condyle spring may

be termed the ramus. The body is pointed anteriorly, and does not reach so far forward as the end of Meckel's cartilage; about a third part of the way back from the anterior end a long oval mental foramen is met with, placed much nearer the upper than the lower border. No sign of any accessory cartilage is met with either at the anterior extremity or in the coronoid process, nor is any to be observed in the angle. The condyle is composed of dense cellular tissue which contains bone in its core, and over this cellular condyle a discus articularis of wedge-shaped form is recognisable, but no joint cavities are present (fig. 7).

No other bone such as one associates with the craninm is as yet ossified.

Comparison between the Crania of Erinaceus and Talpa.

The differences between the cranial and the visceral skeleton of Erinaceus and Talpa are not many, but some are very striking.

The nasal capsule, especially its pars anterior, is relatively shorter in Erinaceus than in Talpa, and there seems to be no foramen epiphaniale perforating the tectum anterius. That in Talpa is very sinuous and difficult to follow.

There is no opercular process on the pars canalicularis of the auditory capsule such as exists in Talpa (Pl. 15).

The Basi-cochlear fissure is absent in Erinaceus.

The cranio-pharyngeal canal remains as a large circular aperture in Erinaceus, but disappears at an early stage in Talpa.

The tectum cranii posterius in Erinaceus is very primitive, resembling much more that of Bos than that of Talpa.

The foramen opticum is surrounded by a cartilaginous ring, of which the lower part is the ala hypochiasmata; in Talpa, owing to the rudimentary condition of the eye muscles, no ala hypochiasmata is present.

As this communication is but part of a series, no attempt has been made to introduce the mass of literature which has made the history of the chondrocranium; only such references are made as directly bear upon the subject. At the end of the series an attempt will be made to summarise the results, and at the same time to point out more precisely how the results confirm or differ from those hitherto obtained in mammals. All the plates, with the exception of 7*a* (which is by my former pupil J. L. Delicati) and those bearing my own initials, are by Mr S. A. Sewell. The figures are by myself. For the embryos represented by the plates and figures I am indebted to Prof. J. P. Hill, Prof. F. Wood Jones, Dr G. Barker, and my former pupil Dr J. H. Morgan.

CHIEF REFERENCES.

VOIT, "Das Primordialcranium des Kaninchens," *Anatomische Hefte*, 1 Abteilung, 116. Heft (Bd. xxxviii., H. 3).

FISCHER, E., "Das Primordialcranium von *Talpa Europœa*," *Anat. Hefte*, Abt. 1, H. 56/57 (Bd. xvii.), 1901.

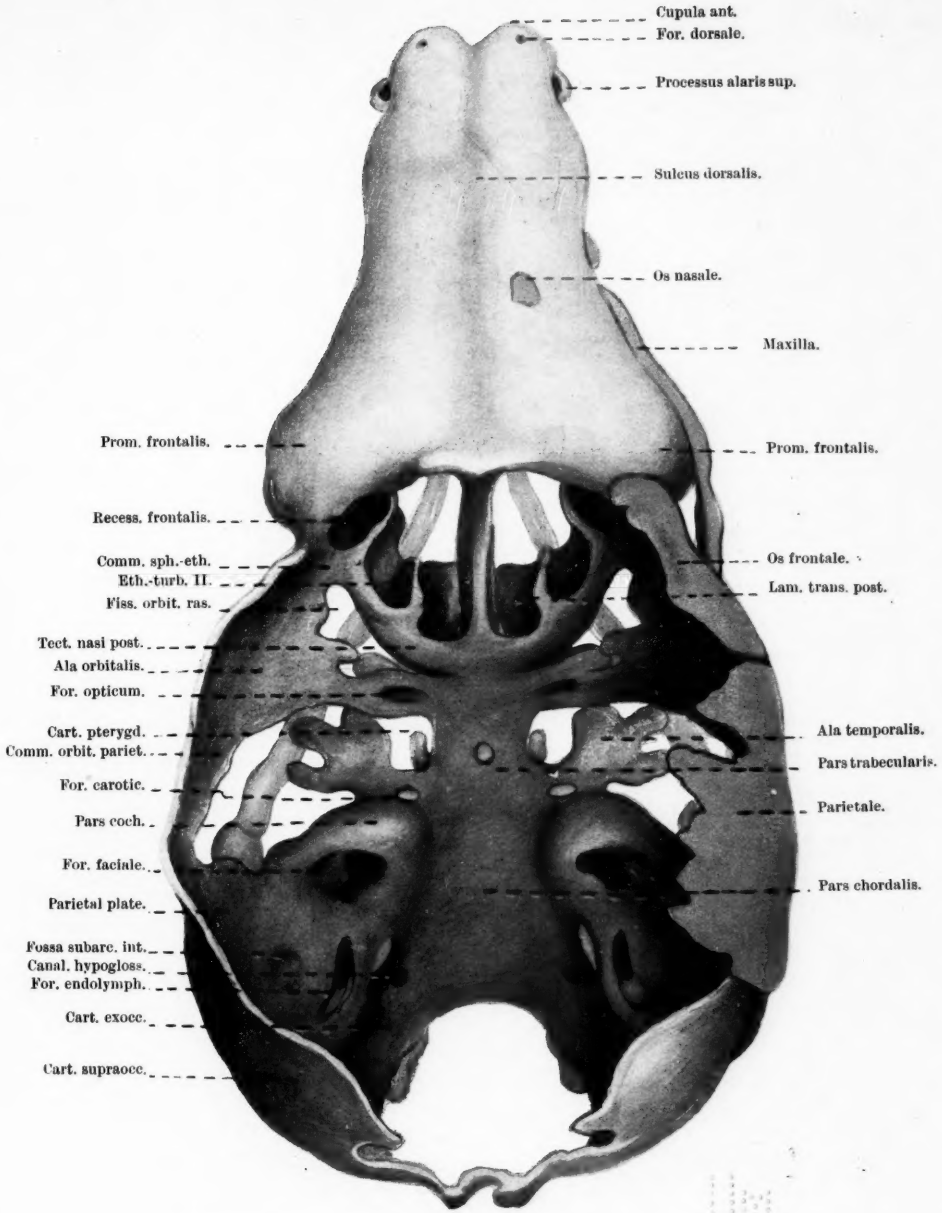
BOLK, "Entwickelungsoorgänge in der occipitalen Region des Primordialcraniums beim Menschen," *Petrus Camper*, Deel ii. Afl. 5, 1904.

FAWCETT, Various communications to *Journal of Anatomy* on chrondocranium, especially the reconstruction of the head of a 30-mm. (Bryce) embryo.

WEBER, *Die Säugethiere.*

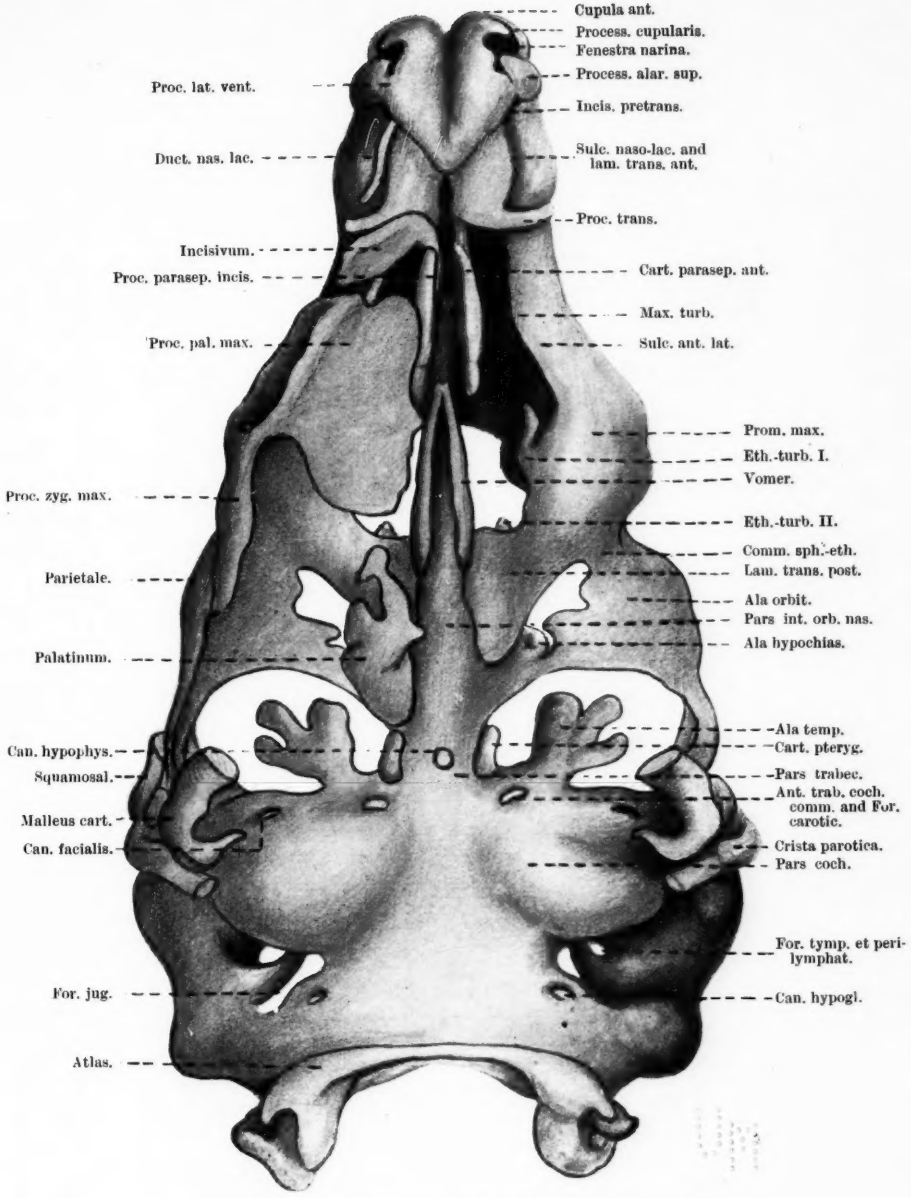
FLOWER and LYDDEKER, *Mammals, Living and Extinct.*

PARKER, W. K., *Phil. Trans. Roy. Soc. London*, 1885.

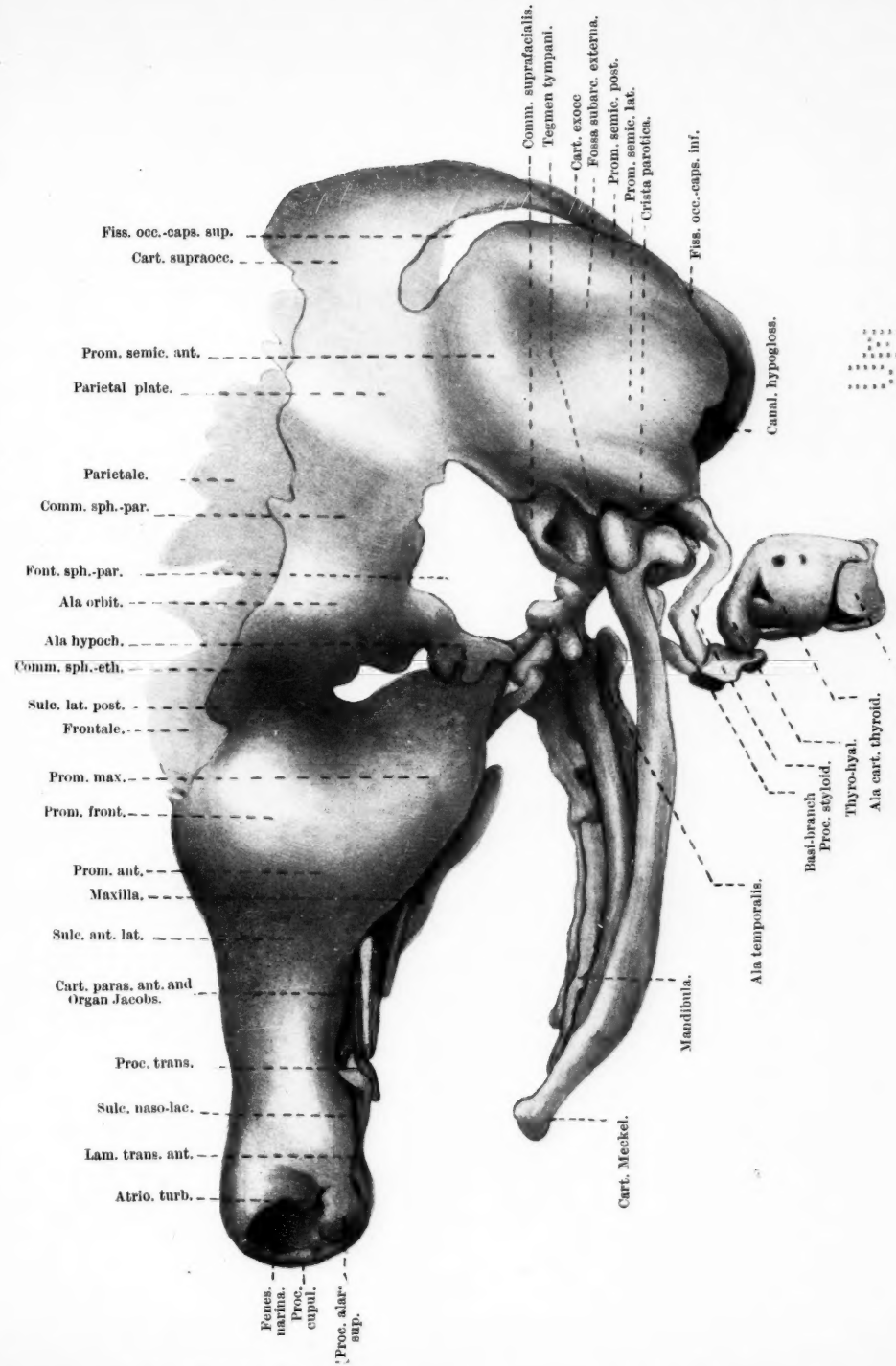


Erinaceus europæus. Chondrocranium of 19-mm. (Hill) embryo, from above.

Professor EDWARD FAWCETT.

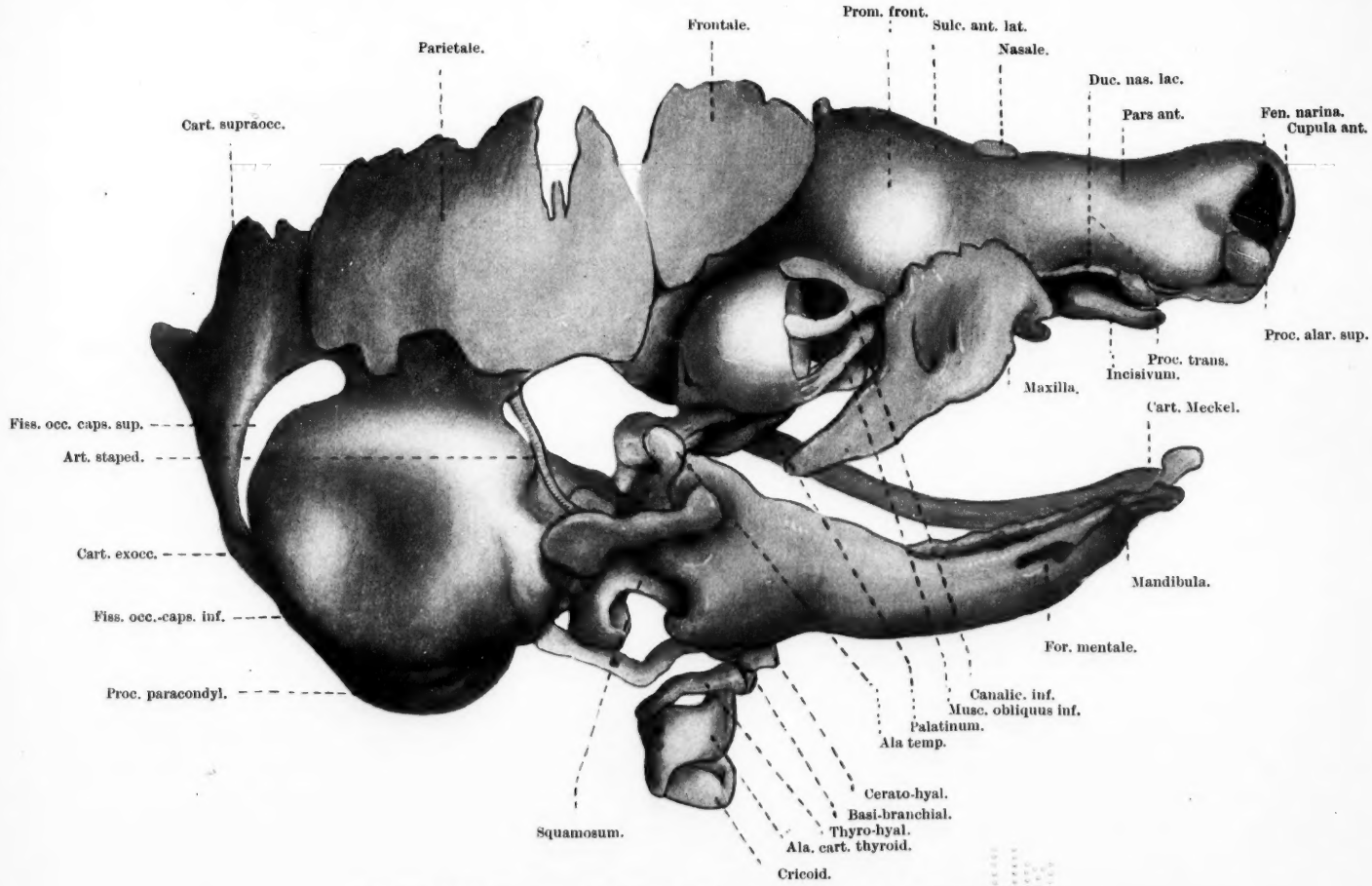


Erinaceus europæus. Chondrocranium of 19-mm. (Hill) embryo, from below.

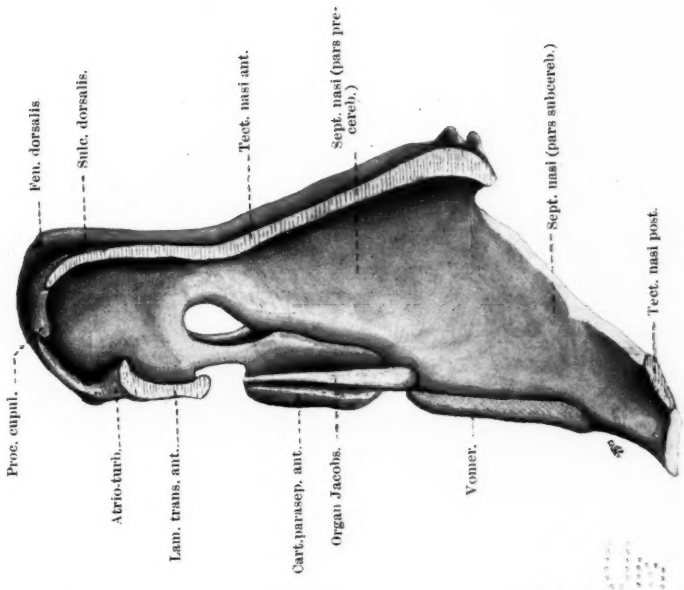


Erinaceus europeus. Left lateral aspect of chondrocranium of 19-mm. (Hill) embryo.

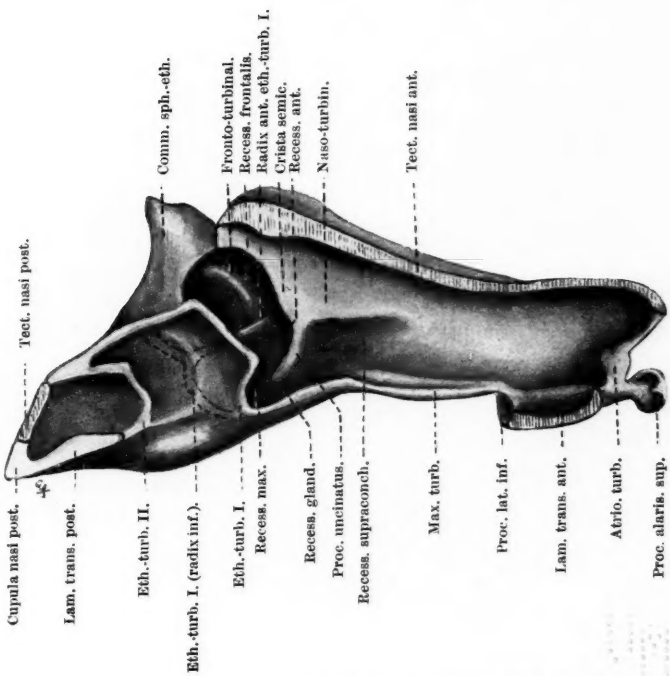
Professor EDWARD FAWCETT.



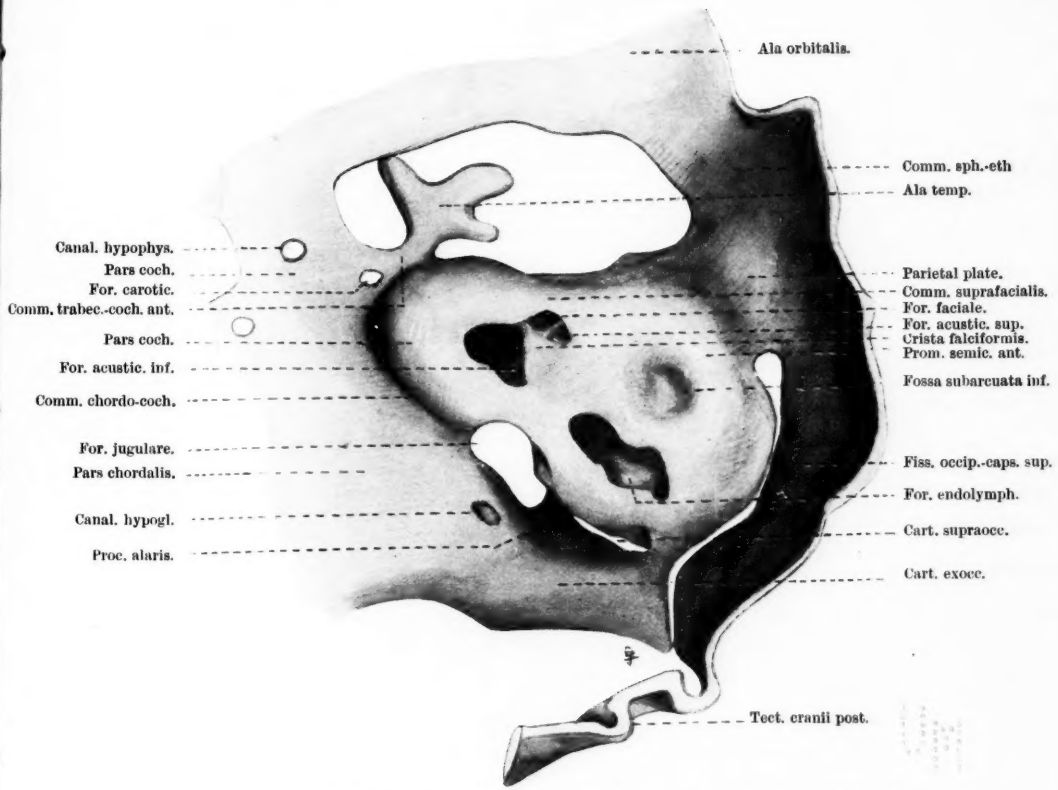
Erinaceus europæus. Right lateral aspect of chondrocranium of 19-mm. (Hill) embryo.



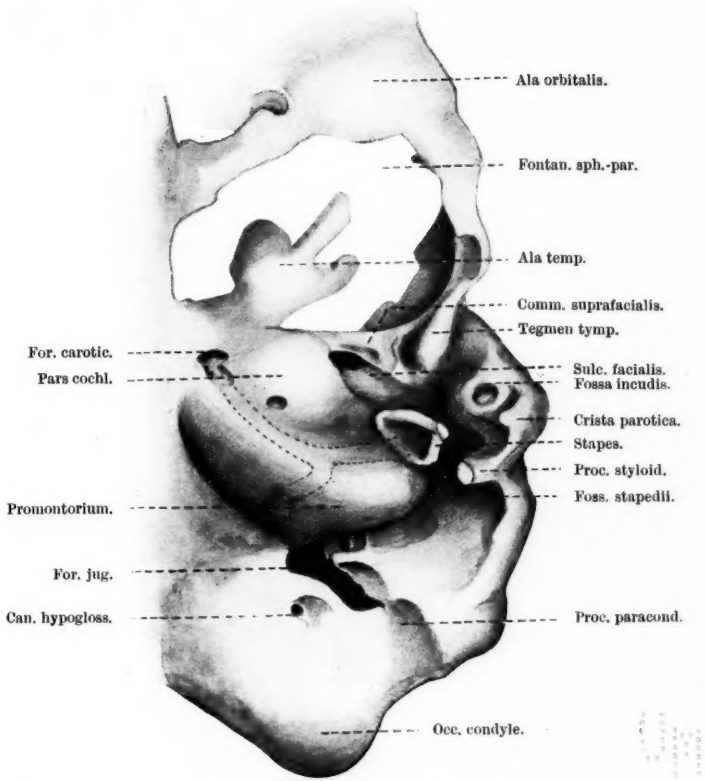
Erinaceus europæus. Septum nasi of 19-mm. (Hill) embryo, from left side.



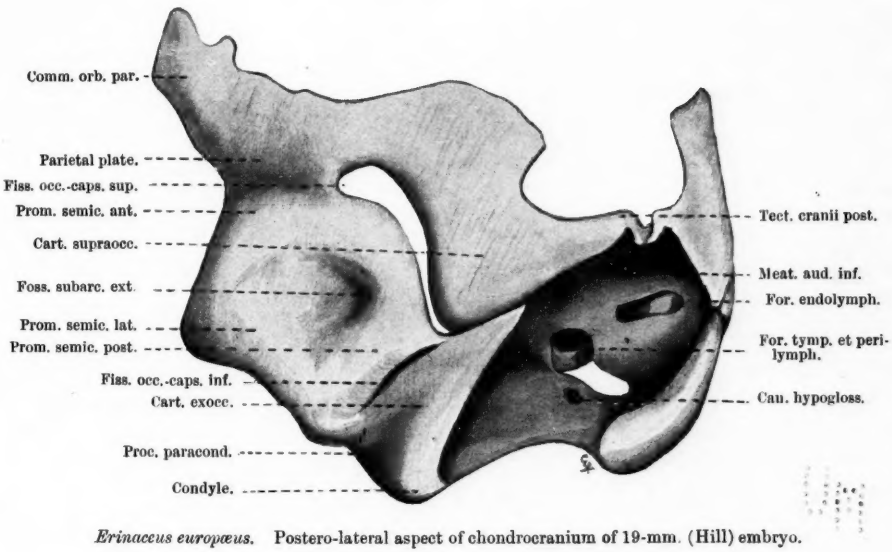
Erinaceus europæus. Medial aspect of left half of nasal capsule of 19-mm. (Hill) embryo.



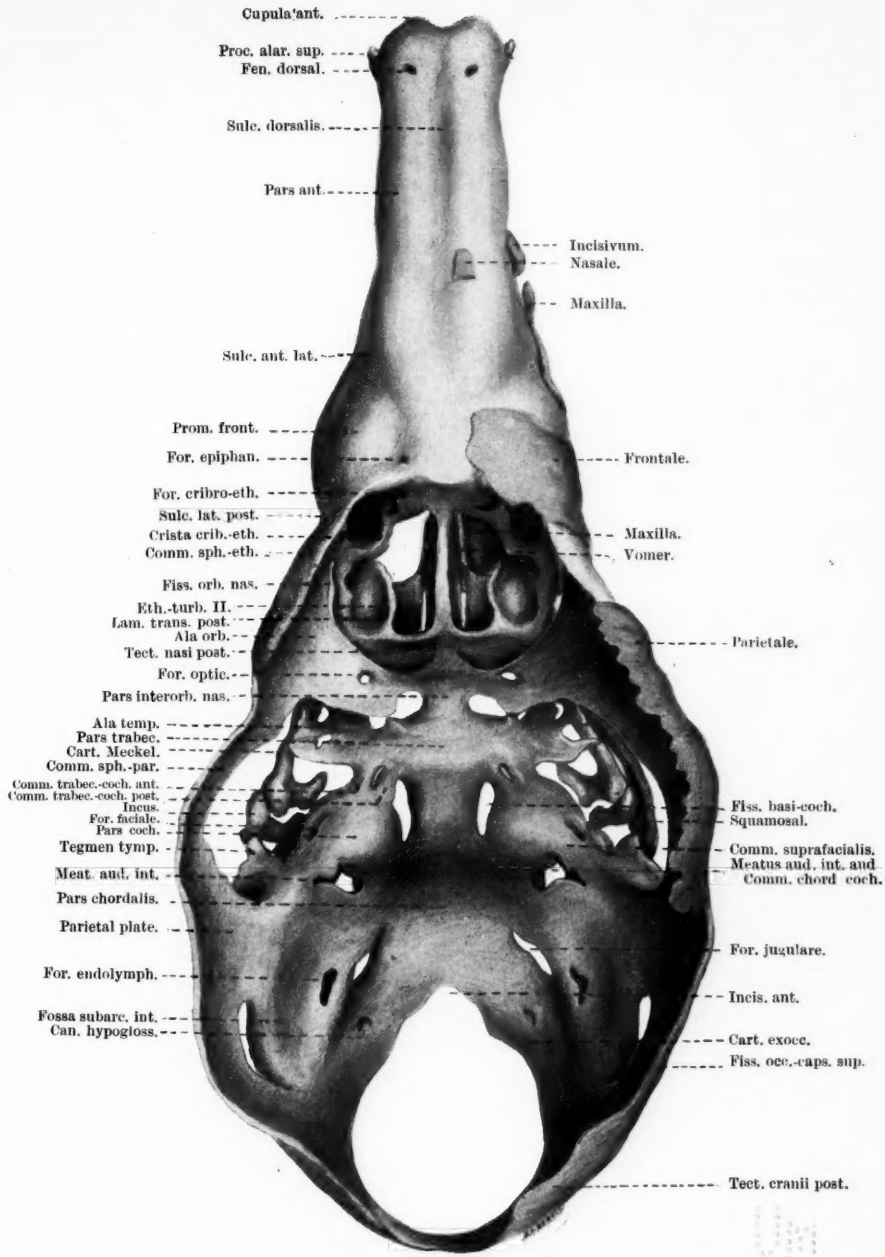
Erinaceus europæus. Medial aspect of right auditory capsule and environs of 19-mm. (Hill) embryo.



Erinaceus europæus. Under aspect of left half of base of chondrocranium of 19-mm. (Hill) embryo.

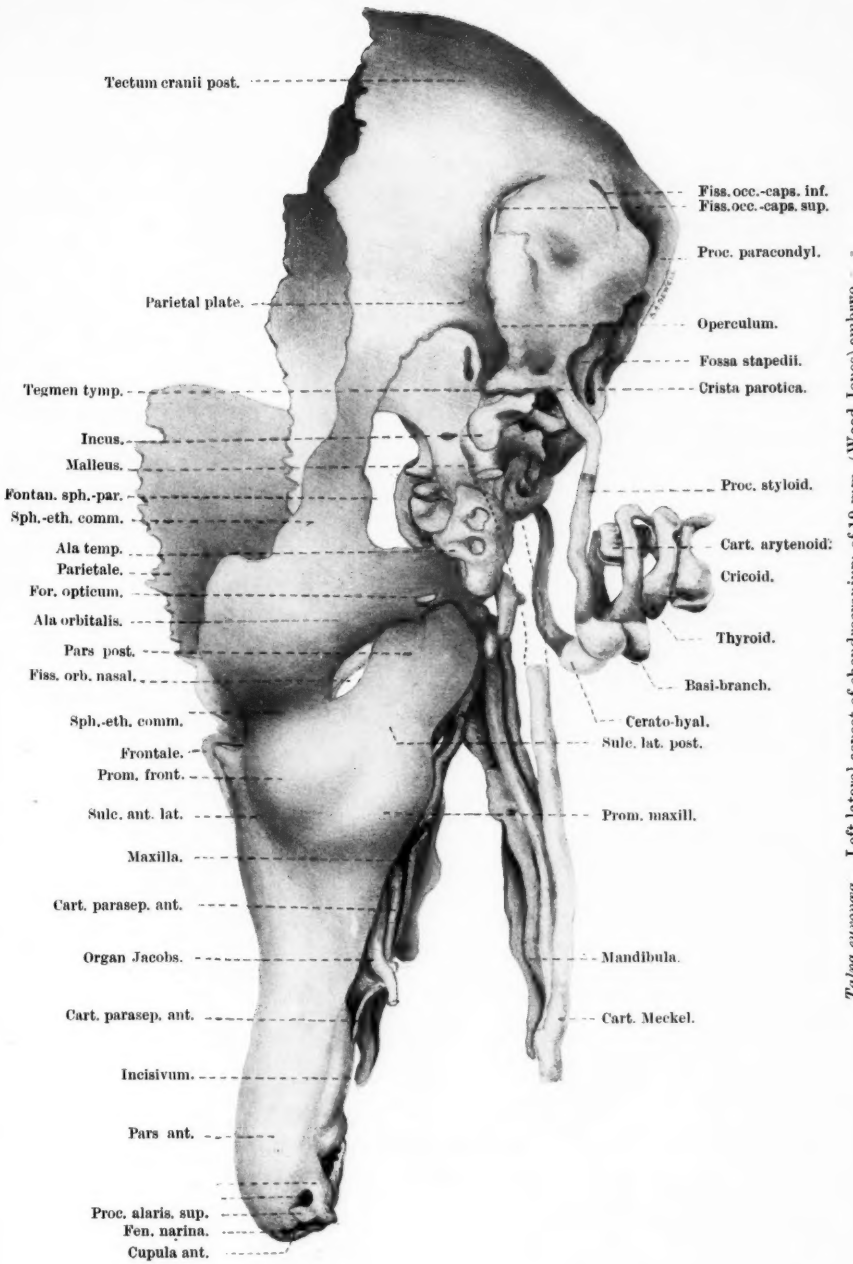


Erinaceus europæus. Postero-lateral aspect of chondrocranium of 19-mm. (Hill) embryo.



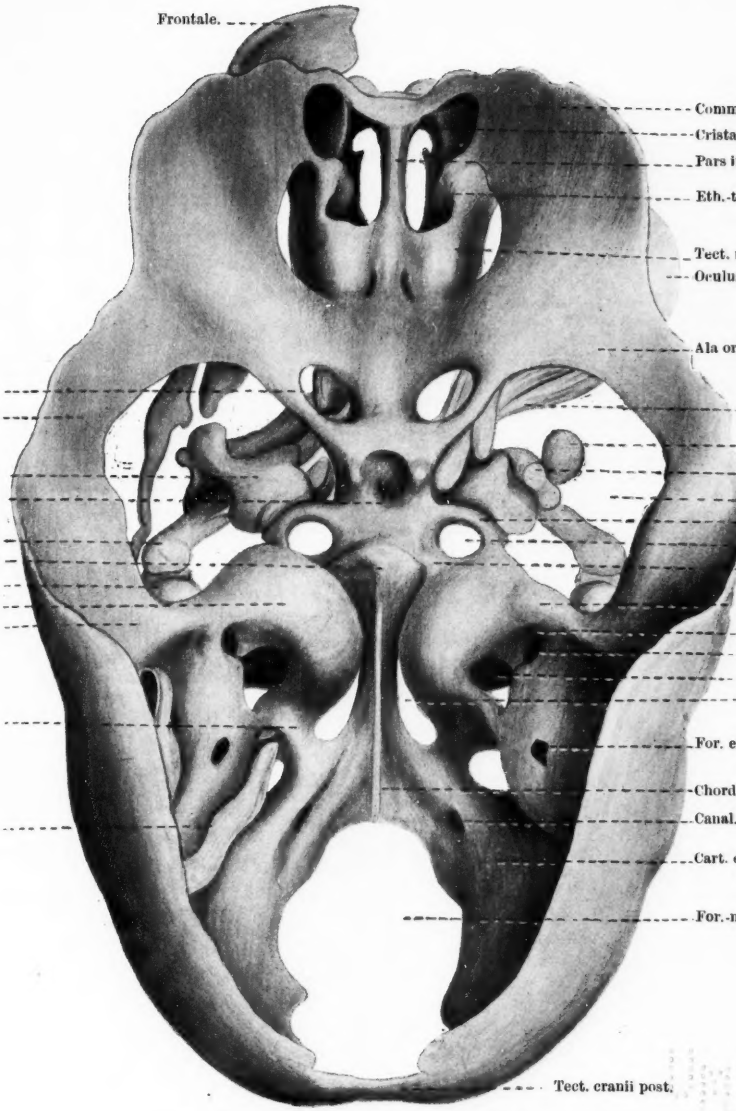
Talpa europæa. Chondrocranium of 19-mm. (Wood-Jones) embryo, from above.

Professor EDWARD FAWCETT.

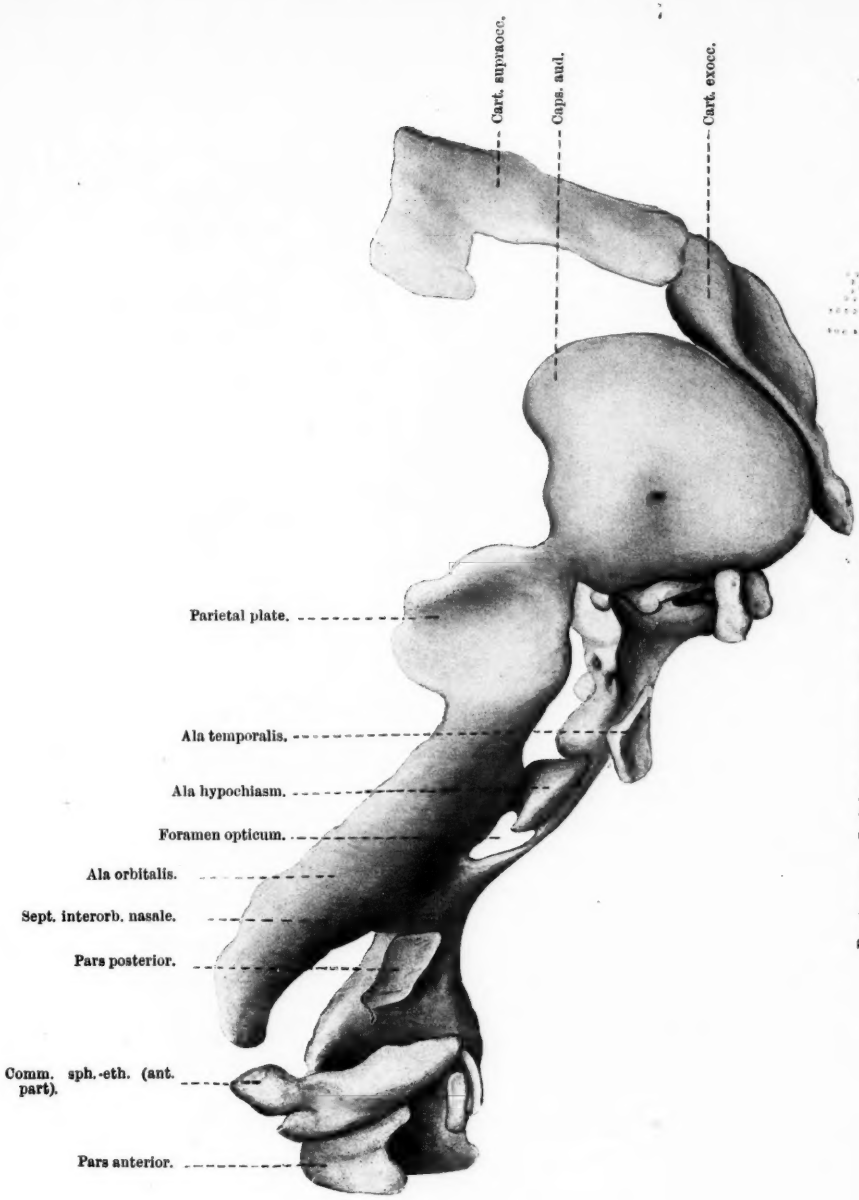


Talpa europæa. Left lateral aspect of chondrocranium of 19-mm. (Wood-Jones) embryo.

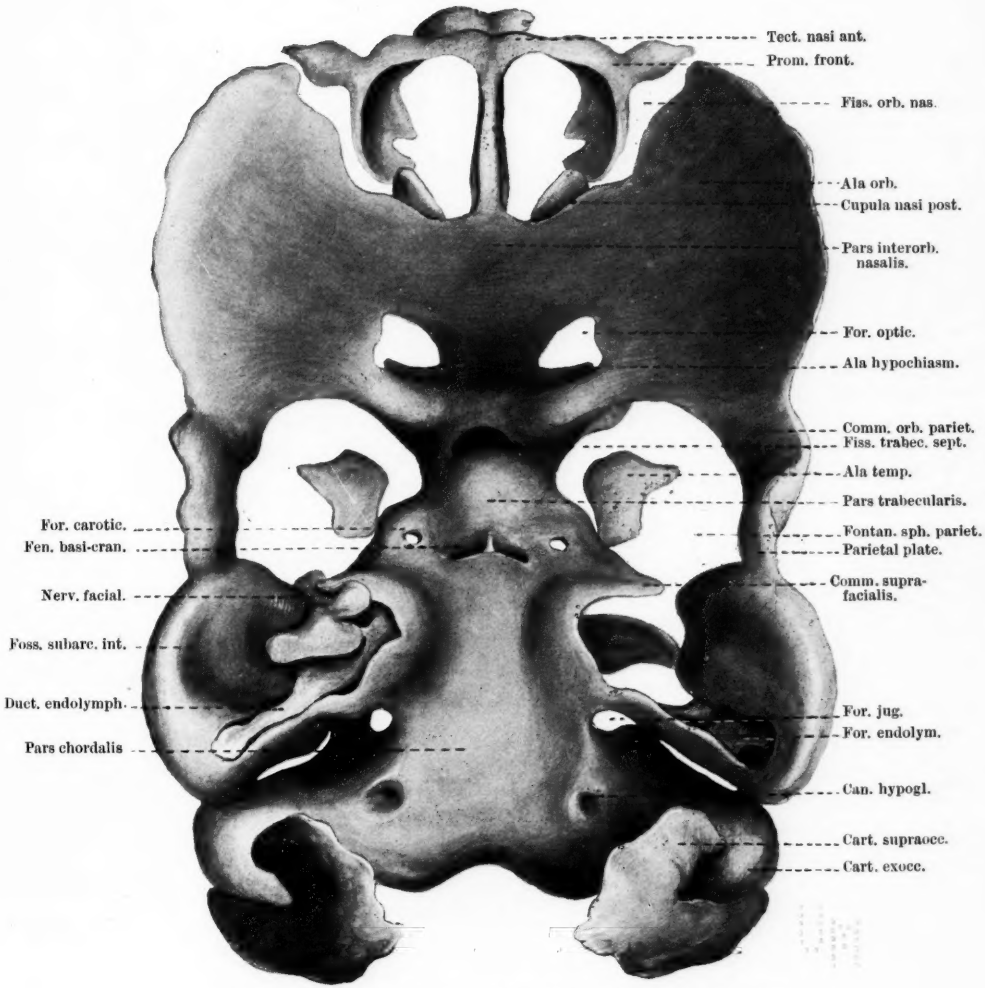
Professor EDWARD FAWCETT.



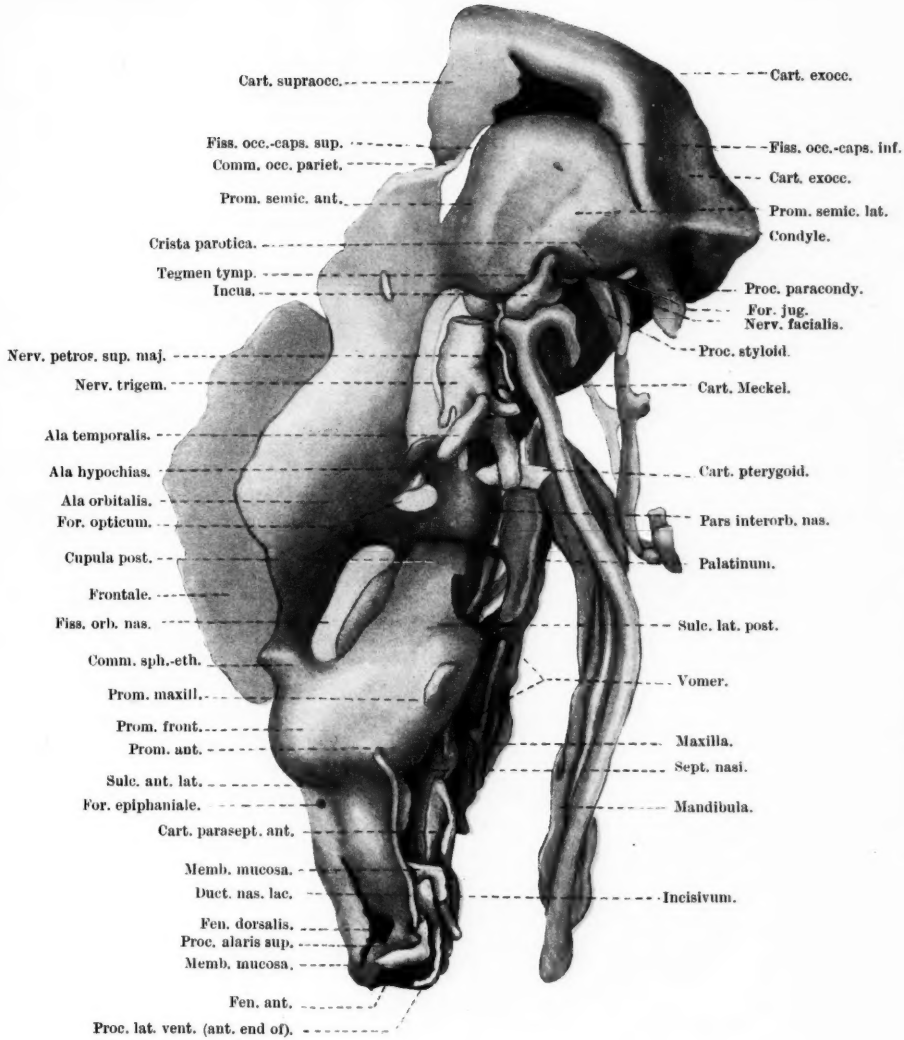
Felis catus. Chondrocranium of 32-mm. (Hill) embryo, from above.



Bos taurus. Left lateral aspect of chondrocranium of 19-mm. (Wood-Jones) embryo.

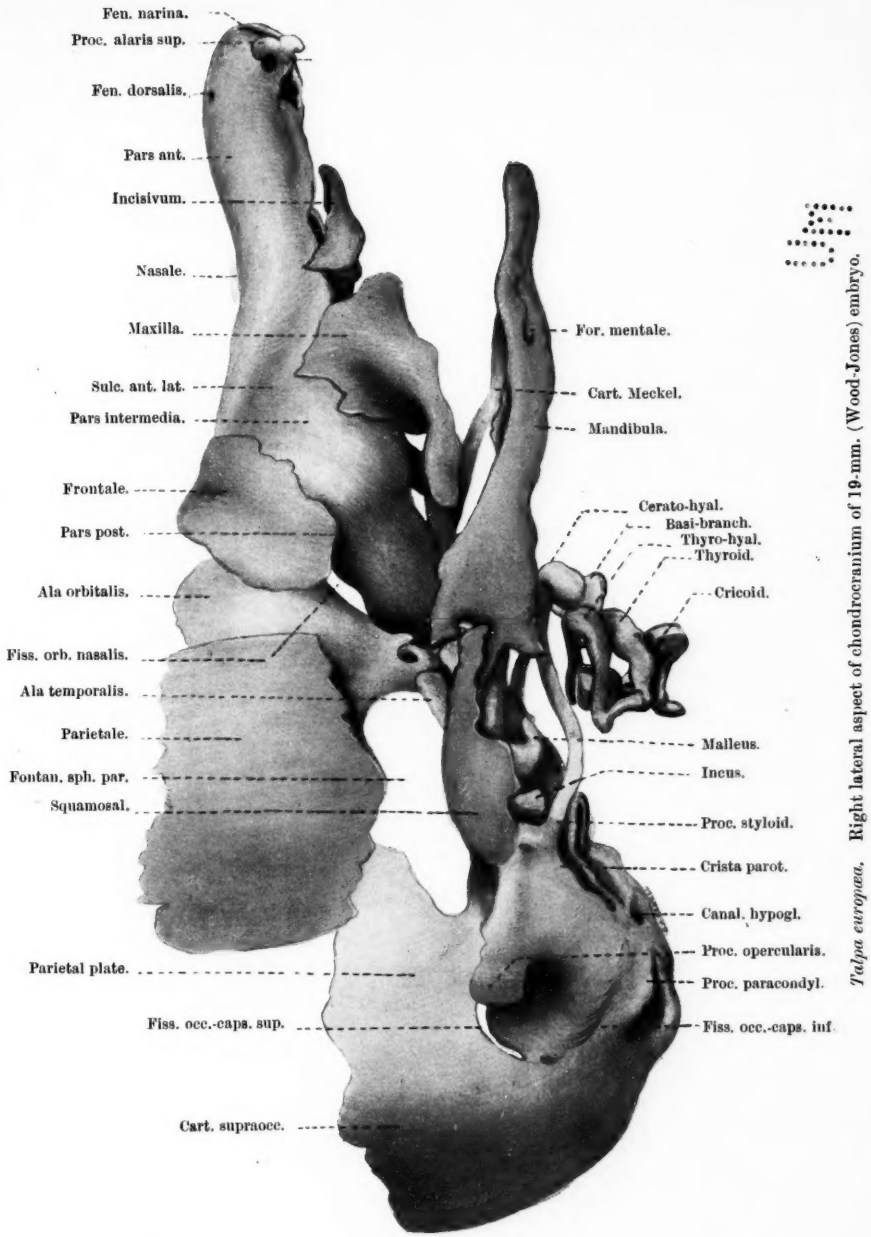


Bos taurus. Upper aspect of chondrocranium of 19-mm. (Wood-Jones) embryo.

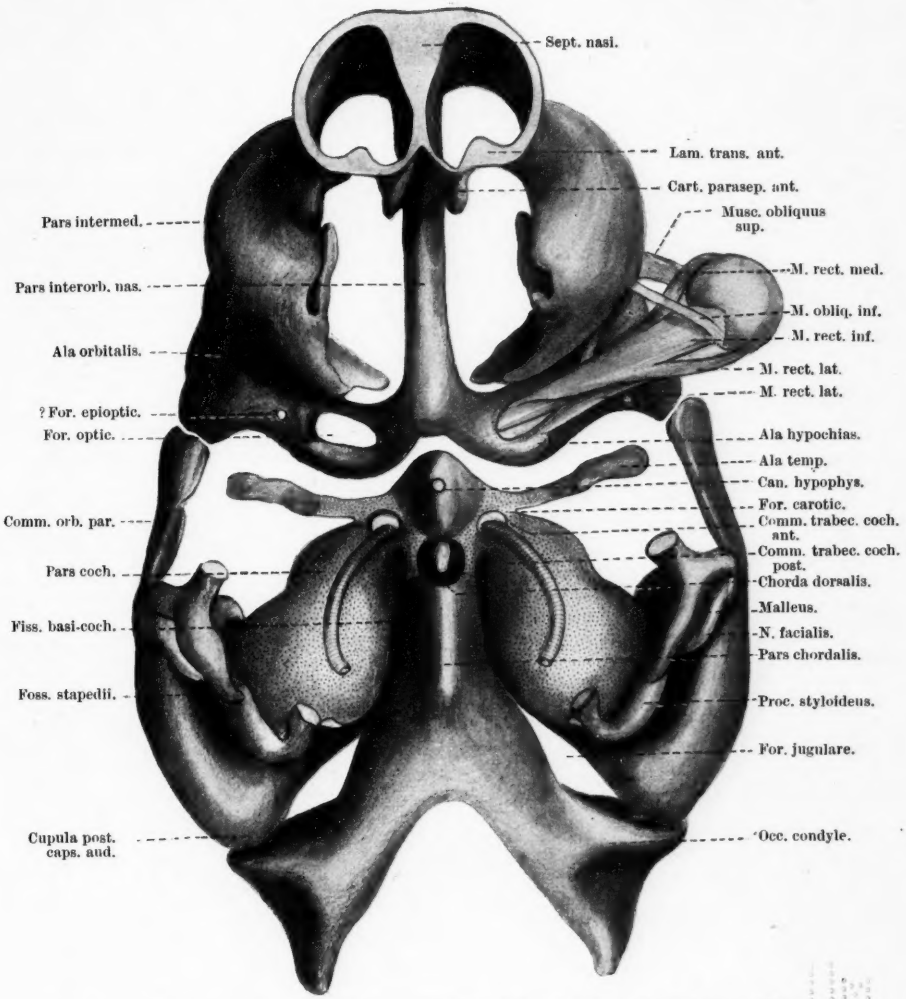


Bos taurus. Left lateral aspect of chondrocranium of 40-mm. (Wood-Jones) embryo.

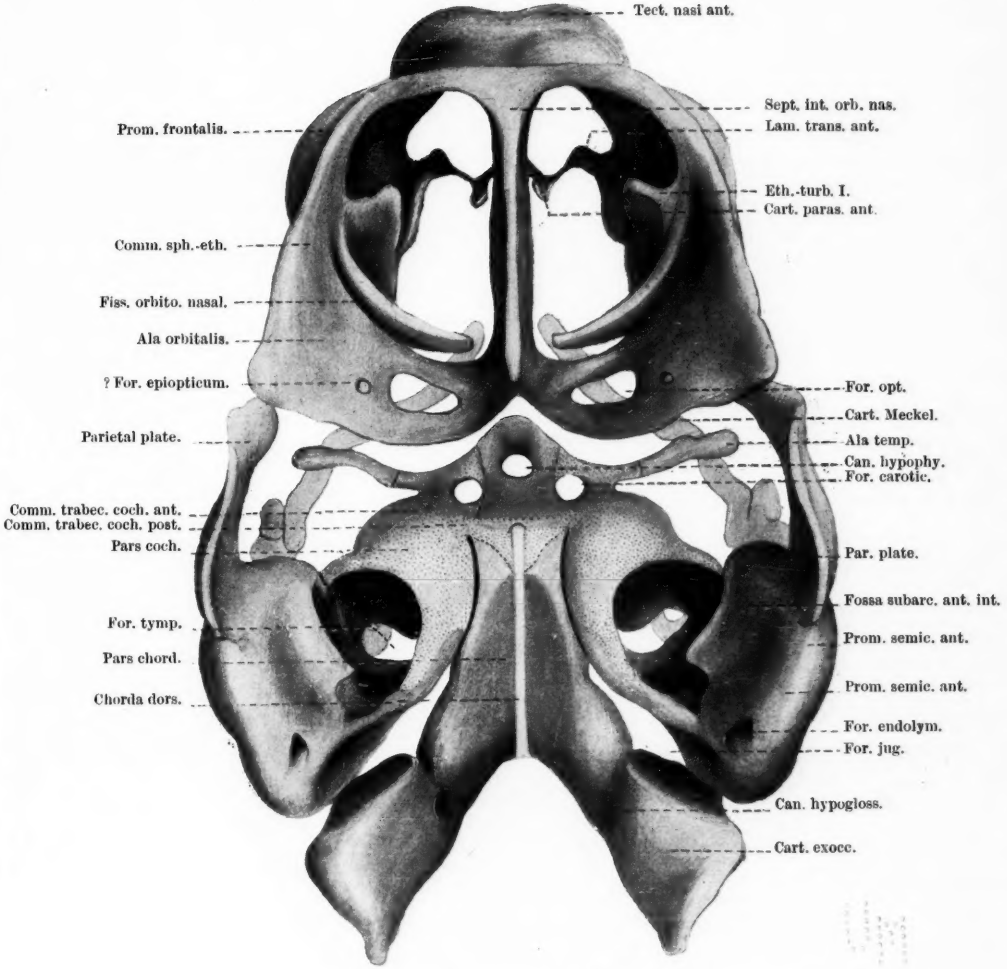
Professor EDWARD FAWCETT.



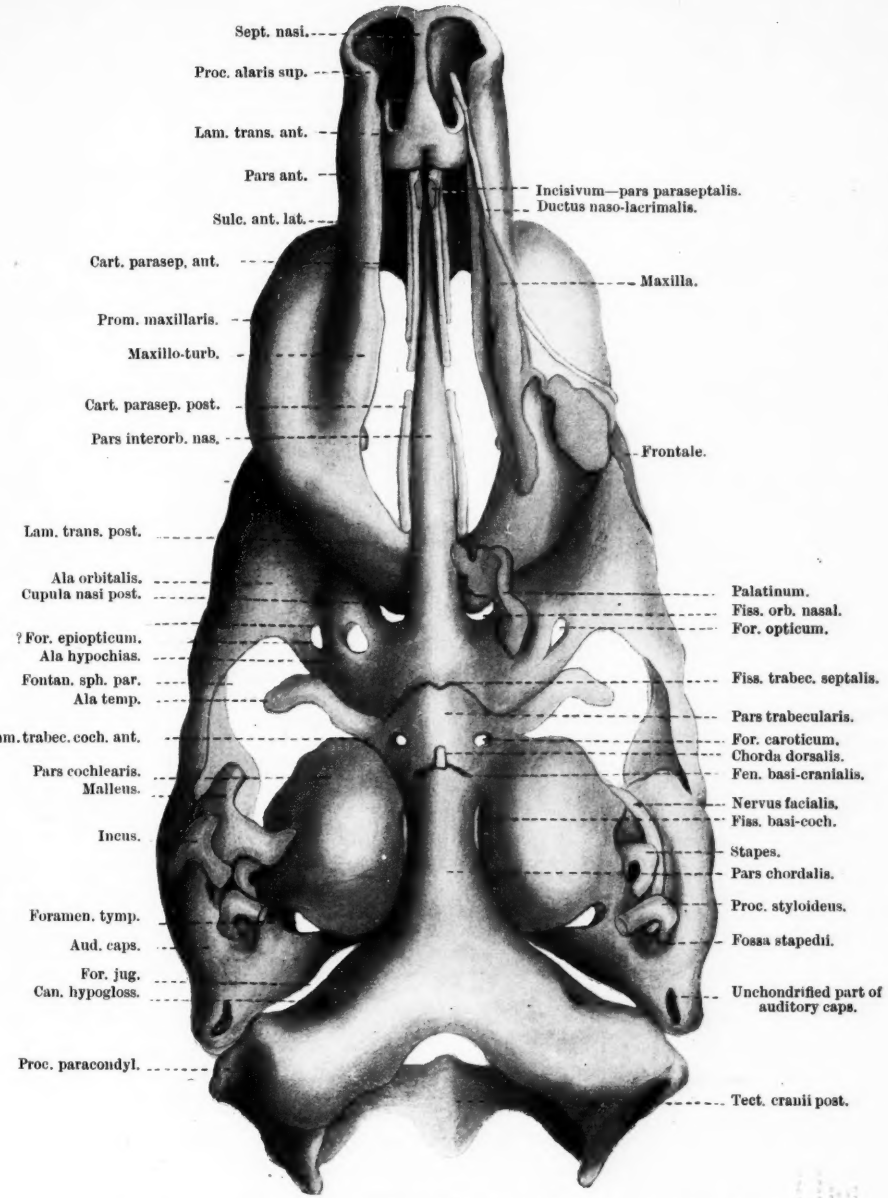
Talpa europæa. Right lateral aspect of chondrocranium of 19-mm. (Wood-Jones) embryo.



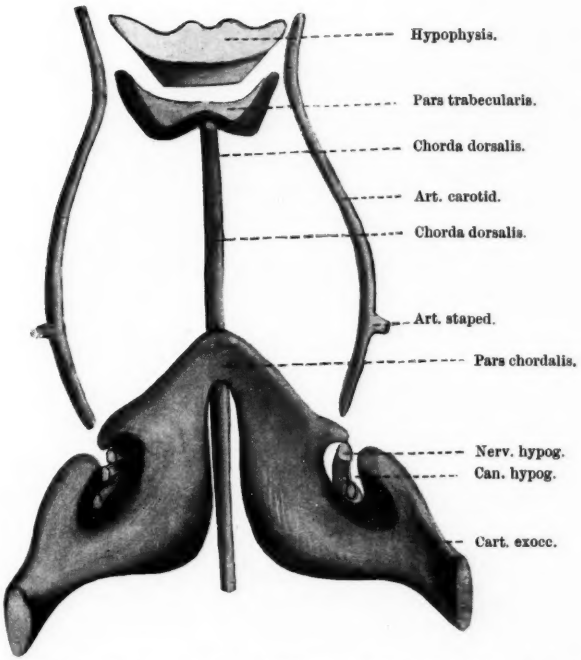
Tatusia novemcincta. Chondrocranium of 12-mm. (Wood-Jones) embryo, from below. The parts dotted are unchondrified, the lamina transversalis anterior and the anterior paraseptal cartilages are procartilaginous.



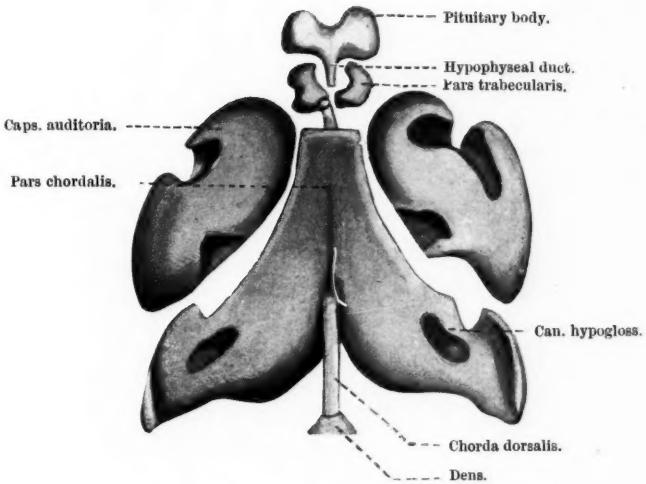
Tatusia novemcincta. Chondrocranium of 12-mm. (Wood-Jones) embryo, from above. Lamina transversalis anterior and anterior paraseptal cartilages are procartilaginous. All areas dotted are as yet unchondrified.



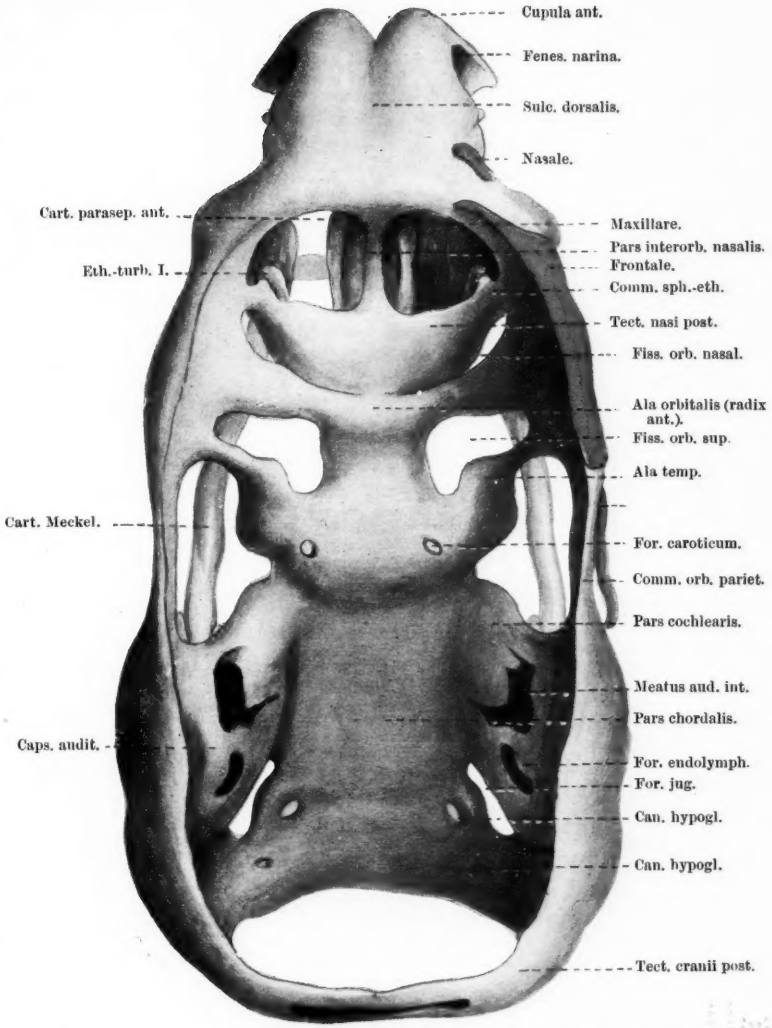
Tatusia novemcincta. Chondrocranium of 17-mm. (Wood-Jones) embryo, from below. The lamina transversalis anterior is unchondrified.



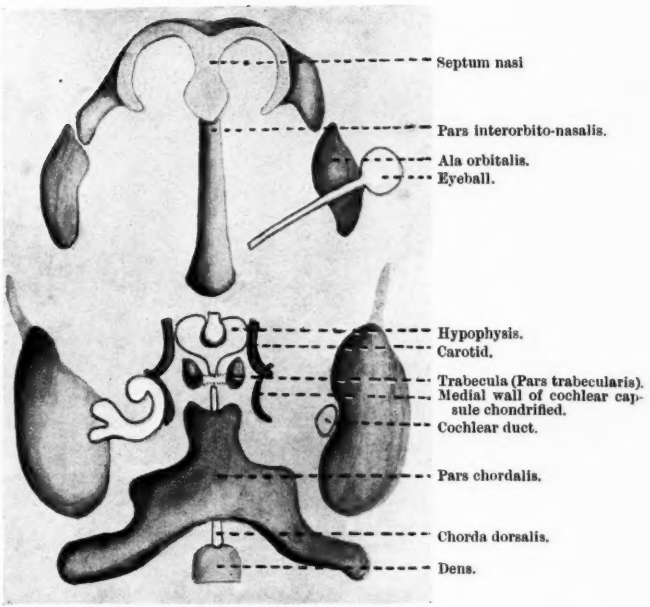
Homo. Chondrocranium of 13·6-mm. (Morgan) embryo, from above.



Homo. Chondrocranium of 14-mm. (Barker) embryo, from above.



Dasyurus viverrinus. Chondrocranium of 9·3-mm. (Hill) embryo, from above.



Talpa. Chondrocranium of 11-mm. embryo, viewed from below.

CONGENITAL STENOSIS OF THE PULMONARY ARTERIAL VALVE, WITH PATENT FORAMEN OVALE, IN AN OLD MAN: WITH REMARKS ON THE VALVULAR FACTOR IN CARDIAC ACTION.[1]

By Alexander Morison, M.D., F.R.C.P.

J. W., aged 72 years, of no occupation, was admitted into the Great Northern Central Hospital on August 31st, 1914, under the care of Dr Tidy in Dr Symes Thompson's wards. He died on September 4th, 1914, and the necropsy took place on the same day.

The clinical notes of the case found are very meagre. The patient appears on admission to have had pain in the right side, with a temperature of 101° Fah., which gradually rose to 104°·6. The pain is stated to have been due to pleurisy, and the patient died, as mentioned, on the fifth day after admission.

The previous history relates that he had had valvular disease of the heart for forty years, and an apoplectic seizure with affection of speech twenty years prior to his death. The diagnosis of his condition recorded is that of right hemiplegia, hæmorrhage into the internal capsule; glaucoma; and congenital disease of the heart. The cardiac diagnosis was probably made after death, and the cerebral condition was probably embolic, as will appear on reading the details of the necropsy, although the head was not examined. There is no mention of the patient's having been cyanotic, but it may reasonably be assumed that he was not.

I accidentally saw the heart in the mortuary and, recognising its interest, directed it to be preserved. I have obtained Dr Symes Thompson's permission to describe the specimen. The examination of the body was made and the following notes taken by Mr Ernest Shaw, M.R.C.P., the Pathologist to the Hospital. I have added some details, which are placed in brackets.

"The body of an obese old man. The head was not examined. *Neck*: tissues very congested; larynx, trachea, and œsophagus natural. *Lungs*: extremely congested, almost black in colour. *Pericardium*: universally and tightly adherent to the heart and great vessels. *Heart*: 16½ ounces; enlarged generally; muscle very soft and a little pale; cavities filled with fluid blood and clots; auricles large and communicating through a very large double opening in the septum. [The actual measurement made in the

[1] Paper read at meeting held on June 29th, 1917.

formalinised heart, which, like other additional measurements stated, may be regarded as less than in the recent specimen, was 3 × 3 centimetres. The loose membranous curtain which should have closed the foramen was perforated by two large openings of about equal size, namely, 15 × 10 millimetres.] The pulmonary arterial valve was conical, with a small opening at the apex; its segments fused, thick, and containing much calcareous material, but without recent change. [The actual size of the stenotic opening was 6 × 6 millimetres. The calcareous change was in the anterior segment of the arterial opening, at a point where the two cusps which formed the valve met. The right auricular wall was very slightly hypertrophied. The coronary sinus was normal, as was the tricuspid valve, the cusps of which were bulged towards the auricle. The wall of the right ventricle was much hypertrophied, measuring, at its thickest, 1½ centimetre, and the length of the cavity from the pulmonary valve to the apex was 7 centimetres. Some shrinkage of the cavity was probably due to formalin.] The aortic and other valves were natural. No vegetations anywhere. [The left auricle was normal, and the wall of the left ventricle at its thickest rather more than 1½ centimetre. That is, the muscular development of the left did not much exceed that of the right ventricle.] The aorta was dilated and slightly atheromatous. The pulmonary artery was large and its walls thin. [This thinness of an unused or comparatively little used vessel has been noted before. The condition of the ductus arteriosus is not mentioned, and the vessels in the specimen are cut off short of its site. The septum ventriculorum is entire.] *Abdomen*: the stomach and intestines are natural; the liver weighed 55 ounces; there was slight thickening of its surface. It was congested and firm. The gall-bladder, pancreas, and suprarenals were natural; the spleen weighed 7 ounces, was large, and contained a large yellow infarct;[1] the kidneys weighed 5 ounces each, were congested, rough, and granular, and showed several small cysts in the cortex. [That is, there was evidence of chronic interstitial nephritis.]

Remarks.—The interest of this case consists in the evidence it affords of a congenital stenosis of the pulmonary arterial valve in a marked degree being not incompatible with long life—the bearer having outlived the allotted span of man—and in the collateral conditions obviating stagnation and promoting circulation, which rendered such longevity possible.

All degrees of closure of the pulmonary arterial orifice occur, from partial stenosis to complete occlusion, which, in its higher degrees, is usually associated with imperfection of the interventricular septum, patency of the

[1] This was probably an old embolism of non-septic character, and argues a like origin for the uninvestigated cerebral lesion.

foramen ovale and permeability of the ductus arteriosus, or with one or other of these conditions.

The nearer the heart approaches to the normal in its ultimate development, naturally the more compatible is the condition with easy circulation and with life. With any considerable degree of mechanical impediment to the outflow of blood from the venous towards the arterial heart, by way of the pulmonary circuit, unless there exists a sufficient collateral avenue, the shorter is the life of the subject. Dr T. B. Peacock, writing in his well-known treatise on *Malformation of the Heart* (2nd ed., 1866, p. 73), states that "the particular situation occupied by the obstruction [of the pulmonary arterial orifice, whether in the conus, at the valves, or in the vessel] is of much less importance . . . than the state of the interventricular septum and the condition of the fœtal passages—the foramen ovale and the ductus arteriosus,—as upon the persistence of one or other of these passages depends the possibility of the circulation being at all maintained.

"In by far the largest number of recorded cases . . . the septum of the ventricles is reported to have been imperfect, so that the aorta derives its blood from both ventricles, thus indicating that the defect at the pulmonic orifice occurred at the early period of fœtal life. When this is the case, the blood readily passes from the right to the left side of the heart and so enters the systemic circulation. In the comparatively few cases in which the obliteration [of the pulmonary orifice] occurs after completion of the septum, the foramen ovale must necessarily form the channel of communication between the two sides of the heart. By this means, however, the circulation is apparently less readily maintained than in the former case, the children in whom such a condition existed having all died very early, while some of those in whom the septum of the ventricles was imperfect survived several years."

In *The Practitioner* for 1888 (p. 112 *et seq.*) I gave details of a very marked case of this kind with imperfect septum ventriculorum, *slight* patency of the foramen ovale, and closure of the ductus arteriosus, which survived, but with marked cyanosis, for seven years. Given, however, sufficient patency of the foramen ovale in such cases, it is questionable whether there would be any advantage over it in a defective interventricular septum. Peacock mentions the case of a young man, 20 years of age, who presented much the same conditions as does the heart I have shown. That is, he had stenosis in a considerable degree of the pulmonary arterial orifice, a patent foramen ovale, and closed interventricular septum. This case would probably have survived longer, had he not died of pulmonary tuberculosis (*op. cit.*, p. 112). Finally, Peacock also mentions

the case of a girl, 16 years of age, who showed definite, but less, contraction of the pulmonary orifice than did the young man referred to, in whom both the interventricular septum and the foramen ovale were closed. She also died of pulmonary tuberculosis (*op. cit.*, p. 122). It is manifest, therefore, that the greater the obstruction at the pulmonary arterial orifice, the more patent must be the collateral avenue towards the left heart to secure easy entrance of the blood into the left heart and relieve that tension of the blood in the chambers of the right heart which has quite appropriately been termed "back pressure." To the *freedom of patency* exhibited by the foramen ovale in the heart of the old man which I have now shown, he undoubtedly owed his long life, the condition of his left heart being normal. The unfortunate meagreness of the clinical notes of this case deprives us of information which might have been interesting. The patient appears only to have been aware of having "valvular disease" of the heart for forty years, which would make him about thirty when that condition was discovered, and it may be assumed that prior to that date he did not suffer much cardiacally. Having apparently become hemiplegic twenty years before death, and probably compulsorily without occupation, he must, during this period, have led a quiet invalid life. The point of importance, however, is that the bearer of the malformation was a well-nourished man in advanced life, who had borne the mechanical cardiac lesion described from his cradle. The renal state was, in all probability, secondary to the circulatory conditions, but may in some measure have contributed to the hypertrophy of the left ventricle, which was, however, not great.

That the *site* of the lesion is an important consideration in this connection is proved by experience. *Obstructive* conditions, in themselves and apart from their degree, appear to be more important up to and including the mitral valve, than are those allowing regurgitation into the right heart and left auricle. Up to this point, blood is entering the central organ of circulation, and propulsion is a less dominant factor than attraction or absorption, which is pulmonary as well as cardiac. In the pulmonary factor in the circulation, attraction is more potent than propulsion, although both forces are exercised; in the cardiac factor the reverse is the case, propulsion is more important than attraction, although here also both forces are in play. Lesions allowing regurgitation from the aorta into the left ventricle, on the other hand, which expose that chamber to increased pressure from the systemic blood column, appear to be, in themselves, more important for the efficiency of the heart than obstruction at the aortic orifice. In this matter, however, the *degree* or amount of the lesion, whether regurgitant or obstructive, has importance. This is testified

by the amount and character of muscular hypertrophy behind the site of the lesion. Even when obstacle to the circulation is essentially vascular, and *not* intracardiac, this point is patent to the pathological anatomist. The ventricle lying behind an aortic aneurism may be absolutely normal in its dimensions if the aortic valve be competent, while a leak in this valve may induce a cardiac hypertrophy, making possible the comparison of the human heart with that of an ox. To gauge the amount or degree of a valvular lesion, and to determine its site, is the task of the clinical physician. The first of these duties requires experience and judgment, and is, even then, a matter of approximate estimation; the signs indicating the site of the lesion are, of course, well known, although not always so easy of interpretation aright as might be supposed.